Fucus serratus, sponges and ascidians on tide-swept lower eulittoral rock

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

Emelia d'Avack and Charlotte Marshall

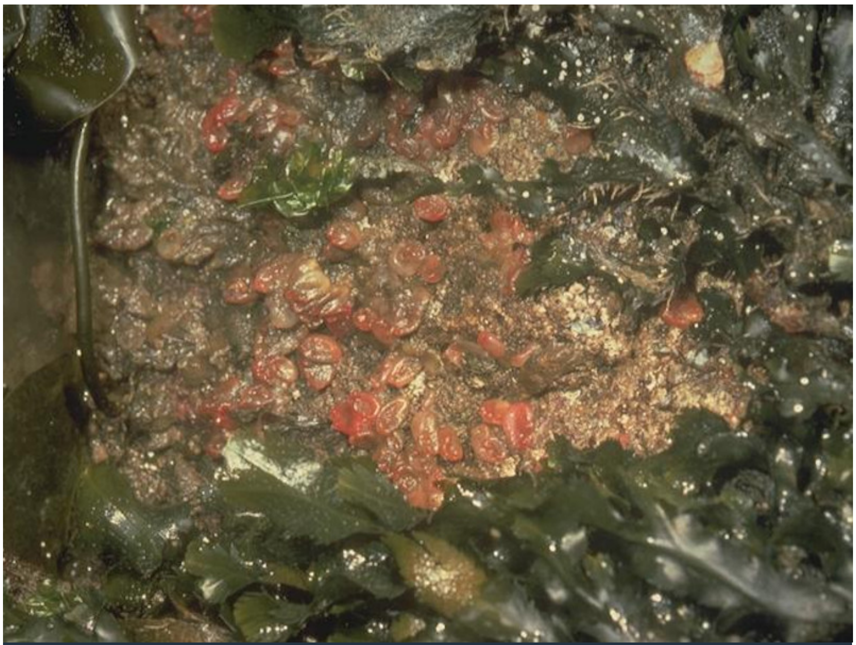
2015-09-25

A report from:
The Marine Life Information Network, Marine Biological Association of the United Kingdom.

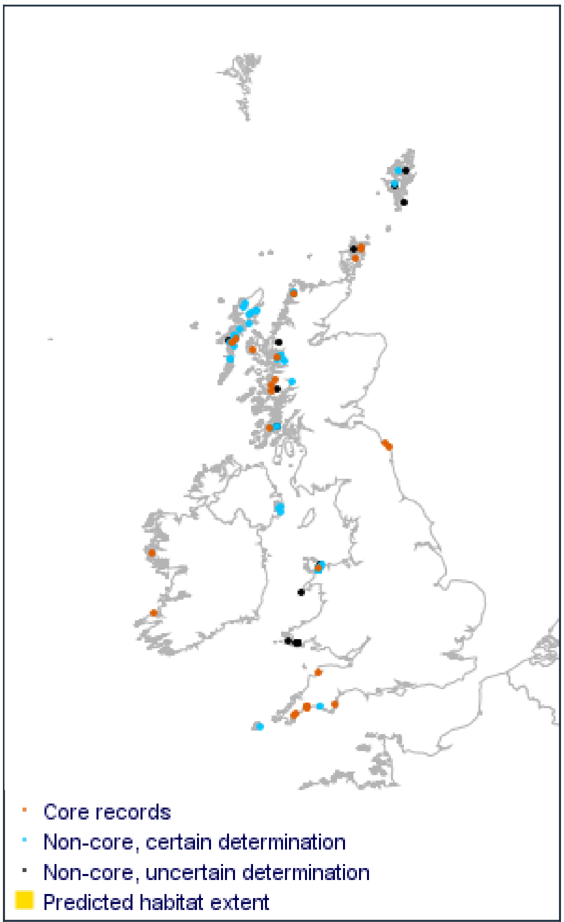
Please note. This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [https://www.marlin.ac.uk/habitats/detail/42]. All terms and the MarESA methodology are outlined on the website (https://www.marlin.ac.uk)

This review can be cited as:
d'Avack, E.A.S. & Marshall, C. 2015. [Fucus serratus], sponges and ascidians on tide-swept lower eulittoral rock. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. DOI https://dx.doi.org/10.17031/marlinhab.42.1

(page left blank)



***Fucus serratus*, sponges and ascidians on tide-swept lower eulittoral rock**
Photographer: Anon.
Copyright: Joint Nature Conservation Committee (JNCC)



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

Researched by Emelia d'Avack and Charlotte Marshall **Refereed by** This information is not refereed.

Summary

UK and Ireland classification

EUNIS 2008	A1.152	*Fucus serratus*, sponges and ascidians on tide-swept lower eulittoral rock
JNCC 2015	LR.HLR.FT.FserT	*Fucus serratus*, sponges and ascidians on tide-swept lower eulittoral rock
JNCC 2004	LR.HLR.FT.FserT	*Fucus serratus*, sponges and ascidians on tide-swept lower eulittoral rock
1997 Biotope	LR.SLR.F.Fserr.T	*Fucus serratus*, sponges and ascidians on tide-swept lower eulittoral rock

Description

Sheltered to extremely sheltered lower eulittoral bedrock, boulders and cobbles that are subject to increased tidal water movement and characterized by the wrack *Fucus serratus* and a rich assemblage of filter-feeding fauna. This community is encouraged by the increased water movement. It includes species such as the sponges *Grantia compressa*, *Halichondria panicea* and *Hymeniacidon perleve*, which occur frequently on steep and overhanging faces. Underneath the *Fucus serratus* canopy is a diverse flora of foliose red seaweeds including *Mastocarpus stellatus*, *Lomentaria articulata*, *Membranoptera alata* and *Chondrus crispus*. The green seaweeds *Cladophora* spp., *Ulva intestinalis* and *Ulva lactuca* and the wrack *Ascophyllum nodosum* are present though usually in small numbers. On the rock underneath the seaweed canopy, species such as the limpet *Patella vulgata*, the barnacles *Semibalanus balanoides* and *Balanus crenatus* and the whelk *Nucella lapillus* can be found though in lower abundance than higher up the shore. Also present on the rock are the tube-forming polychaetes *Spirobranchus triqueter* and spirorbids and more mobile species such as the winkle *Littorina mariae*, the top shell *Steromphala cineraria* and the crab *Carcinus maenas*. Lastly, several species of bryozoans are usually present including *Electra pilosa*, *Flustrellidra hispida* and *Alcyonidium gelatinosum*, all competing for space with the hydroid *Dynamena pumila*, which can form dense populations on the *Fucus serratus* fronds. (Information taken from the Marine Biotope Classification for Britain and Ireland, Version 04.05: Connor *et al*., 2004.).

Depth range

Lower shore

Additional information

-

Listed By

- none -

Further information sources

Search on:

G G G JNCC

Habitat review

Ecology

Ecological and functional relationships

- Due to the moderately strong to very strong currents associated with this biotope, suspension feeders are the dominant trophic group, indicating the importance of a planktonic input to the benthic community. Suspension feeders frequently associated with this biotope include the sponges *Halichondria panicea* and *Hymeniacidon perleve*, ascidians such as *Ascidiella scabra* and *Dendrodoa grossularia*, hydroids including *Dynamena pumila*, bryozoans, spirorbid and serpulid worms, and barnacles.
- Herbivores include the common periwinkle *Littorina littorea*, the grey top shell *Steromphala cineraria* and common limpet *Patella vulgata*. The common periwinkle grazes on microorganisms and fine green algae including *Ulva* sp., apparently rejecting the brown seaweed *Ascophyllum nodosum* (Fish & Fish, 1996). The common limpet can graze on tough plants including *Fucus* sp. and encrusting red algae whereas the grey top shell is unable to consume the tough cell walls and feeds mainly on detritus and microalgae (Fish & Fish, 1996). Grazing by *Patella vulgata* can be an important structuring feature on rocky shores and it is often considered to be a keystone species on north-east Atlantic rocky shores. Reductions in limpet density have been observed to have a significant impact on rocky shore community composition, particularly of fucoid algae and barnacles (Hawkins & Hartnol, 1985; Raffaelli & Hawkins, 1999).
- The common shore crab *Carcinus maenas* is the largest mobile predator frequently associated with this biotope and is likely to move between the boulders and pebbles feeding primarily on small molluscs, especially *Littorina* sp. and *Mytilus edulis*, annelids and other crustacea. It is a true omnivore and will also consume algal material. The predatory mollusc *Nucella lapillus*, the dog whelk, is also frequently associated with this biotope and feeds primarily on the common mussel *Mytilus edulis* and acorn barnacles (Fish & Fish, 1996) such as *Semibalanus balanoides* which may also be found.
- Autotrophs in the biotope are varied and include representatives from the brown, green and red algal groups such as *Fucus serratus*, *Cladophora rupestris* and *Mastocarpus stellatus* respectively. The algae themselves, especially the *Fucus serratus* canopy, may provide substratum for epiphytes including hydroids, sponges and ascidians. The distribution of epifauna into different areas on the *Fucus serratus* is such that competition for space is likely to be reduced. On heavily encrusted *Fucus serratus* fronds tunicates and sponges are largely basally located, most bryozoans, hydroids and spirorbids occur further out on the central parts of the plants whilst *Electra* is predominantly found distally (Seed, 1985). In addition, clumps of algae are likely to provide refuge for smaller crabs and periwinkles which may otherwise be washed away by the strong currents.
- Due to the eulittoral position of this biotope, the associated fauna are likely to experience some predation from larger predators, namely birds, when exposed at low tide and shallow water fish at high tides.

Seasonal and longer term change

The plants in this biotope are likely to experience some seasonal change in abundance, the general pattern being a lower percentage cover over the winter months. Periodic storms may remove older and weaker plants and reduce the overall biomass of the plants. If the forces were strong enough, the cobbles and boulders may also be moved around, to the detriment of the epilithic fauna. For example, if colonies of sponges and ascidians landed face down on the bedrock, parts of the colony may be crushed and lost. However, this biotope is limited to habitats that are sheltered to extremely sheltered from wave exposure and therefore, increases in wave exposure during winter and the occurrence of winter storms are unlikely to affect it to the same extent that more exposed habitats would be affected. In some habitats, the surface cover of *Fucus serratus* may reach 95% in the summer months. Ephemeral green algae especially, increase in abundance over the summer months.

Habitat structure and complexity

The substratum within this biotope is varied and offers a wide variety of potential habitats including bedrock, and the cracks and crevices therein, boulders and cobbles. In addition, the various seaweeds including *Fucus serratus* and foliose red seaweeds such as *Mastocarpus stellatus* offer a substratum for colonization by epiflora including bryozoans, sponges, ascidians and spirorbid worms. 91 taxa of associated fauna were found on 65 specimens of *Fucus serratus* in Strangford Lough, Northern Ireland (Boaden *et al*., 1975). Clumps of seaweed also offer refuge for *Carcinus maenas* and the grazers *Steromphala cineraria* and *Littorina littorea*. The empty shells of the molluscs also provide some heterogeneity to the substratum.

Productivity

Rocky shore communities are highly productive and are an important source of food and nutrients for members of neighbouring terrestrial and marine ecosystems (Hill *et al*., 1998). Rocky shores make a contribution to the food of many marine species through the production of planktonic larvae and propagules which contribute to pelagic food chains.

Raffaelli & Hawkins (1999) reported an estimate of the productivity of intertidal fucoids as 160 gC/m^2/year, although this figure was an estimate for moderately wave exposed habitats. The *Fucus serratus* canopy and other macroalgae associated with this biotope can exude dissolved organic carbon, which is taken-up readily by bacteria and may even be taken-up directly by some larger invertebrates. Dissolved organic carbon, algal fragments and microbial film organisms are continually removed by the sea, which may enter the food chain of local subtidal ecosystems, or be exported further offshore. Many of the species associated with this biotope make a contribution to the food of many marine species through the production of planktonic larvae and propagules, which contribute to pelagic food chains. The productivity in this biotope is likely to be greater than SLR.FserX.T (*Fucus serratus* with sponges, ascidians and red seaweeds on tide-swept lower eulittoral mixed substrata) that is similar is terms of exposure, water flow and species composition but with a mixed substrata as opposed to bedrock.

Recruitment processes

For the majority of important characterizing species and other important species within this biotope, reproduction and recruitment is an annual process. For some of the species, various stages in the reproductive process, including gametogenesis, the timing of spawning and/or recruitment, are variable depending on, for example, environmental factors and geographic location. Recruitment in the major groups present is summarized below.

- Reproduction in *Fucus serratus* commences in late spring and continues until November, with a peak in August and October. Eggs and sperm are produced separately and fertilized externally to form a planktonic zygote. Recruitment is therefore possible from sources outside the biotope.

- *Chondrus crispus* has an extended reproductive period (e.g. Pybus, 1977; Fernandez & Menendez, 1991; Scrosati *et al*, 1994) and produces large numbers of spores (Fernandez & Menendez, 1991). The sexual life cycle of *Mastocarpus stellatus* involves the upright gametophyte plants developing carpospores that settle to produce a tetrasporophyte crust phase. An apomictic cycle has also been noted whereby upright fronds produce carpospores (without fertilization) which give rise to further apomictic plants (Dudgeon *et al.*, 1999). This species (studied as *Gigartina stellata*) had a peak in mature carposporangia in winter in Galway Bay, Ireland (Pybus, 1977). The spores of red algae are non-motile (Norton, 1992) and therefore entirely reliant on the hydrographic regime for dispersal. Hence, it is expected that both *Chondrus crispus* and *Mastocarpus stellatus* would normally only recruit from local populations and that recovery of remote populations would be much more protracted.
- There is some debate as to the nature of reproduction in the breadcrumb sponge *Halichondria panicea* but it is likely that it has a short, annual season of reproduction (see *MarLIN* review).
- *Ascidiella scabra* has a high fecundity and settles readily, probably for an extended period from spring to autumn. Eggs and larvae are free-living for only a few hours and so recolonization would have to be from existing individuals no more than a few km away. It is also likely that *Ascidiella scabra* larvae are attracted by existing populations and settle near to adults (Svane *et al.*, 1987).
- Hayward & Ryland (1995a) and Dons (1927) stated that growth in *Spirobranchus triqueter* is rapid and that sexual maturity is reached in approximately 4 months. Hayward & Ryland (1995a) and Segrove (1941) suggested that breeding probably takes place throughout the year although a breeding peak in spring and summer has been noted and records from Port Erin by Moore (1937) indicated that breeding only took place in April in this location. Castric-Fey (1983) stated that only very rare settlement was observed during winter and maximum settlement occurred in April, June, August and Sept-Oct. Larvae are pelagic for about 2-3 weeks in the summer. However, in the winter this amount of time increases to about 2 months (Hayward & Ryland, 1995a). The settlement of the tubeworm *Spirorbis spirorbis* (studied as *Spirorbis borealis*) on *Fucus serratus* was reported to occur over the summer months in the north east of England (Daly, 1978, cited in Seed *et al.*, 1981).
- *Patella vulgata* become sexually mature as males aged about nine months. Reproduction is an annual process with peaks within a defined spawning season (October - January) depending on location. Planktonic trophic larvae are produced although the larvae are only planktonic for a few days.
- Dispersal of the hydroid *Dynamena pumila* is restricted to the planula stage which usually settles and starts to metamorphose within 60 hours of release (Orlov, 1996). Orlov (1996) that long-distance dispersal was further restricted by the dense bushes of neighbouring algae which serve to trap the larvae in the area. Seed *et al.* (1981) reported that the reproductive zooids of *Dynamena pumila* were in abundance between May and August in Strangford Lough, Northern Ireland.
- The larvae of *Alcyonidium gelatinosum* have only a brief planktonic life and brooding of the embryos has been reported from several localities during spring or autumn (Fish & Fish, 1996).

Time for community to reach maturity

No information was found concerning the development of this biotope. However, the important characterizing species all reach sexual maturity within a few years and have annual reproductive episodes suggesting that the time taken for the community to develop is likely to be less than five years. However, if adverse environmental conditions prevail, time taken to reach maturity could take significantly longer.

Additional information

-

Preferences & Distribution

Habitat preferences

Depth Range	Lower shore
Water clarity preferences	
Limiting Nutrients	Data deficient
Salinity preferences	Full (30-40 psu), Variable (18-40 psu)
Physiographic preferences	Enclosed coast / Embayment, Strait / sound
Biological zone preferences	Lower eulittoral
Substratum/habitat preferences	Bedrock, Cobbles, Large to very large boulders, Small boulders
Tidal strength preferences	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Strong 3 to 6 knots (1.5-3 m/sec.), Very Strong > 6 knots (>3 m/sec.)
Wave exposure preferences	Extremely sheltered, Sheltered, Very sheltered
Other preferences	Moderately strong to strong tidal flows.

Additional Information

This biotope is associated with sheltered to extremely sheltered habitats.

Species composition

Species found especially in this biotope

Rare or scarce species associated with this biotope

-

Additional information

The MNCR recorded 393 species in 56 records of this biotope, although not all of the species occurred in all records of the biotope (JNCC, 1999).

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

This biotope is characterized by the macroalgae *Fucus serratus* and a rich assemblage of filter-feeding fauna encouraged by moderately strong to very strong tidal currents. The filter feeding communities include the sponges *Halichondria panacea*, *Grantia compressa* and *Hymeniacidon perleve* as well as the sea squirts *Ascidiella scabra* and *Dendrodoa grossularia*. Underneath the *Fucus serratus* canopy is a diverse flora of foliose red seaweeds including *Chondrus crispus* and *Lomentaria articulata*. Other species such as the limpet *Patella vulgata* and the tube building worm *Spirobranchus triqueter* are also present.

Fucus serratus is the key structuring species as the macoalgae form a canopy within this biotope that provides protection from desiccation for the various underlying foliose red seaweeds in addition to providing a substratum for a diverse range of epifauna. Characterizing elements of this biotope are sponges, ascidians and red seaweeds in particular *Halichondria panacea Ascidiella scabra* and *Chondus chrispus.* The sensitivity assessments consider the characterizing species that define this biotope; *Fucus serratus*, sponges and ascidians. Loss/degradation of the *Fucus serratus* population would thus result in direct loss/degradation of the associated community and significantly alter the character of the biotope. Therefore, the assessments typically emphasise the sensitivity of *Fucus serratus*.

Resilience and recovery rates of habitat

The loss of *Fucus serratus* canopy will have both short and long-term consequences for associated benthic communities, resulting in the loss of biogenic habitat, reduction in diversity, simplification of vertical structure and reduction or loss of ecosystem functioning such as primary productivity (Lilley & Schiel, 2006). The removal of macroalgae canopy exposes understory species to sunlight and aerial conditions during low tides resulting in bleaching and eventual die backs. Through time, some functional groups, such as low-lying turfing algae, recover and reach greater abundance compared to prior disturbance conditions (Bulleri *et al*., 2002; Bertocci *et al*., 2010). These turf algae can then prevent canopy recovery by inhibiting recruitment. Schiel & Foster (2006) observed long-term demographic lags in recovery after important losses of fucoids. Recovery of lost or severely reduced species can be slow, with species replacement common. Indeed loss of fucoids can cause systems shifts to a state dominated by low-lying turf or filamentous ephemeral algae (Airoldi *et al*., 2008; Mangialajo *et al*., 2008; Perkol-Finkel & Airoldi, 2010). Turf algae, especially corallines, are often highly resilient and positively associated with perturbed areas. The changes in dominant species and community structure take some time to develop and, although some effects occur rapidly, many are manifested over a period of several years (Schiel & Lilley, 2011). Hawkins & Southward (1992) found that, after the *Torrey Canyon* oil spill, it took between 10 and 15 years for the *Fucus* sp. to return to 'normal' levels of spatial and variation in cover on moderately exposed shores. Therefore, for factors that totally destroy the biotope, recovery is likely to be low.

Fucus serratus is dioecious, perennial and reproduces sexually. Reproduction commences in late spring/early summer and continues through summer and autumn, peaking in August - October. Eggs and sperm are released into the water and fertilization occurs in the water column. The zygote then develops into a minute plant that can then settle onto the substratum. Arrontes (1993) determined that the dispersal of *Fucus serratus* gametes and fertilized eggs was restricted to within 1–2 m from the parent. Average annual expansion rates for *Fucus serratus* have been estimated at 0.3 to 0.6 km per year (Coyer *et al*., 2006; Brawley *et al*., 2009). Dispersal is highly limited as the negatively buoyant eggs are fertilized almost immediately after release and dispersal by rafting reproductive individuals is unlikely (Coyer *et al*., 2006). *Fucus serratus* does not float, and thus mature detached individuals cannot transport reproductive material to distant sites as might be the case for other brown algae. However *Fucus serratus* is found on all British and Irish coasts so there are few mechanisms isolating populations. While poor dispersal is true for medium or large spatial scales (hundreds of metres to kilometres), recruitment at short distances from parental patches is very efficient, as most propagules settle in the vicinity of parent plants (Arrontes, 2002).

Chondrus crispus has an extended reproductive period (e.g. Pybus, 1977; Fernandez & Menendez, 1991; Scrosati *et al*., 1994) and produces large numbers of spores (Fernandez & Menendez, 1991). Recovery of a population of *Chondrus crispus* following a perturbation is likely to be largely dependent on whether holdfasts remain, from which new thalli can regenerate (Holt *et al*., 1995). In addition, the spores of red algae are non-motile (Norton, 1992) and therefore entirely reliant on the hydrographic regime for dispersal. Hence, similar *to Fucus serratus*, *Chondrus crispus* would normally only recruit from local populations slowing down the recovery of remote populations. Minchinton *et al.* (1997) documented the recovery of *Chondrus crispus* after a rocky shore in Nova Scotia, Canada, was totally denuded by an ice scouring event. Initial recolonization was dominated by diatoms and ephemeral macroalgae, followed by fucoids and then perennial red seaweeds. After 2 years, *Chondrus crispus* had re-established approximately 50% cover on the lower shore and after 5 years it was the dominant macroalga at this height, with approximately 100% cover. Minchinton *et al.* (1997) concluded that although *Chondrus crispus* was a poor colonizer, it was the best competitor.

The larvae of the sea squirt *Ascidiella aspersa* have a short free-swimming planktonic stage. Fertilization to settlement and metamorphosis is estimated to only take about 24 hours at 20°C (Niermann-Kerkenberg & Hofmann, 1989). The congener *Ascidiella scabra* has a high fecundity and settles readily, probably for an extended period from spring to autumn. Svane (1988) describes it as 'an annual ascidian' and demonstrated recruitment onto artificial and scraped natural substrata. It is also likely that *Ascidiella scabra* larvae are attracted by existing populations and settle near to adults (Svane *et al*., 1987). Fast growth means that a dense cover could be established within about 2 months. However, if mortality occurs at a time when larvae are not being produced, other species may settle and dominate in the freed spaces.

The settlement of new colonies of the breadcrumb sponge *Halichondria panicea* is likely to occur within one year with growth rate ranging from 0.1 to 0.4 cm^2/day. Knowlton & Highsmith (2005) found a rapid response to tissue damage from nudibranch grazing with the sponge recovering within 4 weeks from grazing impacts.

Resilience assessment. *Fucus serratus* is the main structural species as its removal will lead cause the decline of associated species and eventually to a change towards a different biotope. If the entire population of *Fucus serratus* is lost other species may come to dominate. Where resistance is 'None', then resilience is 'Low' based on the low long-distance dispersal range of *Fucus serratus*. Re-establishment of the seaweed may depend on the ability to out-compete other species and this may be dependent on suitable environmental conditions. Upon arrival, the success of the new population is explained by: (1) rapid establishment of monospecific patches in the immediate vicinity of the founding plants, (2) high colonization rates of disturbed areas, (3) the ability to recruit to undisturbed canopies, (4) the ability to outgrow resident canopy species (particularly *Fucus vesiculosus*) and (5) the increase in size and number of dispersal centres (Arrontes, 2002).

If some of the population remains it is unlikely that other species will come to dominate due to efficient recruitment of *Fucus serratus* over short distance. Removal of some of the adult canopy will allow the understorey germling to grow faster. Recovery will probably have occurred after a year. Therefore when resistance is ‘Medium’, recovery will be very fast resulting in a ‘High’ resilience score due to very efficient colonization of areas adjacent to *Fucus serratus* patches. If resistance is assessed as ‘High’, resilience is automatically ‘High’ as there are not impacts to recover from.

Strong tidal currents, characteristic of this biotope, encourage communities of sponges and ascidians. Changes to the hydrological regime are therefore likely to directly influence the presence of these species. Once removed, these species are however likely to rapidly recolonize due to planktonic larvae thereby facilitating recruitment. Most species associated with this biotope are poor long distance dispersers. However the moderately strong tidal currents of this biotope enable these species to disperse over greater distances than in slow flowing environments.

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

Hydrological Pressures

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

Most fucoids are cold-temperate species (Lüning, 1984), and temperatures above 20°C are generally considered unsuitable (Zou *et al.*, 2012). The effect of high temperature stress on photosynthesis in brown algae is related to inactivation of enzymes and the induction of reactive oxygen species (ROS), leading to photoinhibition (Suzuki & Mittler, 2006). Growth rates of adult brown macroalgae may be affected by temperature through the increase in metabolic rates (Nygard & Dring, 2008). However, *Fucus serratus* is found along the Atlantic coast of Europe from Svalbard to Portugal and on the shores of north-east America. The seaweed is thus well within its thermal range in the British Isles.

Increased temperature (>15°C) can enhance biotic stress on *Fucus* plants by increasing mico- and macrofouling rates (Wahl *et al.*, 2010). Several studies observed adverse effects of *Fucus serratus* as a result to warm thermal stress in terms of growth, physiological performance and reproductive output in Spain and Portugal (Pearson *et al.*, 2009; Viejo *et al.*, 2011; Martínez *et al.*, 2012). Jueterbock *et al.* (2014) however determined that these negative impacts can be explained by within-population genetic diversity. Southwest-Ireland and Brittany are hot-spots of genetic diversity (Coyer *et al.*, 2003; Hoarau *et al.*, 2007) and may thus be more resilient to changes in temperature. Indeed, Nielsen *et al.* (2014) found no negative effects on growth rates of adult *Fucus* *serratus* to water temperatures of 22°C (laboratory experiment with specimen collected from Firth of Forth, Scotland). Phenotypic plasticity plays therefore an important role in determining the sensitivity of individual populations to changes in temperature.

The geographical ranges of a variety of associated species such as *Halichondria panicea*, *Chondrus crispus* and *Ascidiella scabra* suggest that these organisms will be tolerant to a change in temperature at the pressure benchmark. It is however possible that acute changes in temperature will have adverse effects resulting in mortalities.

Sensitivity assessment. An increase in 5°C above average British and Irish temperatures is not likely to have a detrimental effect of *Fucus serratus* and associated communities, however, phenotypic plasticity will influence the tolerance of individual population. Resistance and resilience are therefore both assessed as 'High' (no impacts to recover from). The biotope group is 'Not Sensitive' to a change in temperature at the pressure benchmark.

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

Lüning (1984) reported that *Fucus serratus* survived in the laboratory for a week a range temperature between 0°C and 25°C. *Fucus serratus* is found along the Atlantic coast of Europe from Svalbard to Portugal and on the shores of north-east America. The seaweed is thus well within its thermal range in the British Isles. Lüning (1984) placed this species in his 'Cold temperature North Altantic group'.

Sensitivity assessment. A decrease in acute or chronic temperature above average British and Irish temperatures is not likely to have a detrimental effect of *Fucus serratus* and associated communities, based on global distribution. However, it should be noted that phenotypic plasticity will influence the tolerance of individual population. Resistance and resilience are therefore both assessed as 'High' (no impacts to recover from). The biotope group is 'Not Sensitive' to a change in temperature at the pressure benchmark.

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

This biotope group is found in the intertidal and is therefore likely to experience cyclical periods of hypo- and hyper-salinity. Seaweeds are able to compensate for changes in salinity by adjusting internal ion concentrations. However this will occur at a cost, reducing photosynthetic rate and hence affecting the growth rate of the seaweed. Growth rates for *Fucus serratus* are maximal at a salinity of 20 psu with the critical limit for recruitment set at 7 psu (Malm *et al.*, 2001).

Sensitivity assessment. *Fucus serratus*, commonly inhabit narrow fjords where salinity can vary widely along a spatial (kms) and/or temporal (hours to daily) scale. Species associated with this biotope are therefore likely to be tolerant to an increase in salinity from 35 to 40 units for one year. No direct evidence was found on the effects of hypersaline (>40 units) conditions. However, hypersaline conditions may result in damage to the fucoid but loss of associated community (e.g. ascidians and sponges). Therefore a tentative resistance of 'Medium' is recorded, at low confidence. Resilience is probably 'High', so that the biotope is probably of 'Low' sensitivity at the pressure benchmark.

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

This biotope group is found in the intertidal and is therefore likely to experience cyclical periods of hypo- and hyper-salinity. Seaweeds are able to compensate for changes in salinity by adjusting internal ion concentrations. However this will occur at a cost, reducing photosynthetic rate and hence affecting the growth rate of the seaweed. Growth rates for *Fucus serratus* are maximal at a salinity of 20 psu with the critical limit for recruitment set at 7 psu (Malm *et al*., 2001).

Sufficient salinity is essential for successful fertilization and germination in *Fucus* (e.g., Brawley, 1992; Serrão *et al*., 1999). Malm *et al*. (2001) found that fertilization success in *Fucus serratus* decreased substantially with strongly reduced salinity. Indeed the study found that fertilization success was 87% at 9 psu but declined to 5% at 6 psu. Reduced salinity also affects dispersal by decreasing swimming performance of fucoid sperm (Serrão *et al*., 1996).

Other characterizing species associated with this biotope are likely to be tolerant of a reduction in salinity. *Halichondria panacea*, *Chondrus crispus* amd *Ascidiella scabra* can all be found in reduced salinity conditions. *Patella vulgata* can endure periods of low salinity and was found to die only when the salinity was reduced to 3-1 psu (Fretter & Graham, 1994). However, Little *et al*. (1991) observed reduced levels of activity in limpets after heavy rainfall and in the laboratory activity completely stopped at 12 psu.

Sensitivity assessment. At the level benchmark a reduction in salinity of from full to variable or reduced in one year could have beneficial effects *on Fucus serratus* as growth rates are maximal below full saline conditions. Other characterizing species associated with this biotope are also tolerant of reduced salinity at the level of the benchmark. Resistance and resilience are therefore both assessed as 'High' (no impacts to recover from). The biotope is therefore 'Not Sensitive'.

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

The rich community of suspension feeders in this biotope is, in part, due to the strong tidal streams with which it is associated. Strong currents provide suspension feeder with a continual supply of food and removes sediment that would otherwise interfere with their feeding apparatus. A decrease in water flow rate could lead to siltation, to the detriment of filter feeders. Furthermore, grazers unable to cope with the strong flow rates normally associated with this biotope may be able to graze more efficiently, increasing herbivory pressure. High water flow rates increases 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 organisms attached to the algae are also lost. Fucoids are however highly flexible and are able to reorientate their position in the water column to become more streamlined. By going with the flow, fucoids can reduce the relative velocity between algae and the surrounding water, thereby reducing drag and lift (Denny *et al*., 1998). Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). In addition, increased water flow will cause scours though increased sediment movement affecting in particular small life stages of macroalgae by removing new recruits from the substratum and hence reducing successful recruitment (Devinny & Volse, 1978) (see 'siltation' pressures). Changes in water motion can thus strongly influence local distribution patterns of Fucus spp. (Ladah et al., 2008). Increases in drag can however be counterbalanced in the long-term by changes in morphology resulting in structurally more resistant thalli and holdfasts (Haring *et al.*, 2002).

Sensitivity assessment. Strong tidal flow, characteristic of this biotope, encourages communities of sponges and ascidians. Changes to the hydrological regime are therefore likely to directly influence the presence of these species. As the biotope occurs in very strong tidal flow (>3 m/s) an increase in water flow is unlikely. A reduction in water flow is likely to result in a loss of the suspension feedeing species, an overall reduction in species richness, and result in loss of this biotope, as it is replaced by another *Fucus serratus* dominated biotope, e.g. LR.LLR.F.Fserr.FS. However, a change of 0.1-0.2 m/s(the benchmark) is unlikely to adversely affect the biotope, although a reduction may decrease feeding and hence growth rates. Therefore, a resistance of 'High' is recorded, with a resilience of 'High' and a sensitivity of 'Not sensitive' at the benchmark level.

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

This biotope group is found in the intertidal and is therefore subjected to cyclical immersion and emersion. *Fucus serratus* and *Chondrus crispus* are both intertidal species adapted to a degree of periodic desiccation. *Fucus serratus* is more susceptible to desiccation than other *Fucus* species located further up the shore and subjected more frequently to aerial exposure (Schonbeck & Norton, 1978). The critical water content for *Fucus serratus* is estimated at 40% with water losses past this point causing irreversible damage. Beer *et al*. (2014) found that *Fucus serratus* could not regain any positive photosynthetic rates after rehydrating from 10% water content. In addition, early life history stages will be more susceptible than adults (Henry & Van Alstyne, 2004). Germlings are however protected from desiccation by the canopy of adults. A study by Brawley & Jonhnson (1991) showed that germling survival under adult canopy was close to 100% whereas survival on adjacent bare rock was close to 0% during exposure to aerial conditions.
The *Fucus* canopy is also likely to protect other underlying species to a great extent. Mortalities of other component of the community will however occur if the canopy is removed (see ‘abrasion’ pressure). Mathieson & Burns (1971) measured the photosynthetic rate of *Chondrus crispus* at varying degrees of desiccation and found that after loss of 65% of its water content, the rate of photosynthesis dropped to 55% of the control rate. In *Palmaria palmata*, 50% of the plant's water content can be lost in less than 4 hours in dry air at 25°C (Kain & Norton, 1990). This scenario can reasonably be expected at low tide in summer in Britain, although the *Fucus* canopy is likely to protect the underlying red algae to some extent. The upper shore extent of *Fucus serratus* and *Chondrus crispus* may be replaced by species more tolerant of desiccation and more characteristic of the mid-eulittoral such as *Fucus vesiculosus* or *Ascophyllum nodosum*.

A decrease in submergence is likely to adversely affect the suspension feeder population by reducing feeding opportunities as immersion is a prerequisite of feeding. This can prove fatal for short lived species such as bryozoans and ascidians. The tissue of *Halichondria panicea* holds some water and can tolerate a certain degree of desiccation. On the other hand, the soft bodied sea squirt *Ascidiella scabra* has a greater vulnerability to this pressure. The sea squirt is commonly found in damp crevices or under the canopy of macroalgae offering protection from desiccation but individuals at the highest point on the shore may dry out and die at the benchmark level.

On the other hand, an increase in submergence is likely to benefit this biotope. Feeding opportunity for suspension feeders will increase; desiccation and temperature stresses for all flora and fauna will decrease as will predation from birds. The biotope may extend further up the shore but this extension is likely to be counteracted by a reduction in the lower shore extent of the biotope likely to be taken over by seaweeds more characteristic of the sublittoral fringe. Furthermore, predation by the common shore crab *Carcinus maenas* is likely to increase.

Sensitivity assessment. Severe desiccation and associated osmotic stress can increase mortality in *Fucus serratus* (Pearson *et al*., 2009). Other species better able to tolerate desiccation will competitively displace *Fucus serratus* following changes in emergence regime. The characterizing species of this biotope are largely protected from extreme levels of desiccation by the macroalgal canopy. However, the increase in emergence will result in loss of the extent of the biotope up the shore. Therefore, resistance is thus assessed as 'Low', resilience assessed as 'Medium', and the biotope assessed as 'Medium' sensitivity to changes in emersion regime at the level of the benchmark.

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

Fucus serratus is highly flexible but not physically robust and an increase in wave exposure will cause mechanical damage, breaking fronds or even dislodging algae from the substratum. Fucoids are permanently attached to the substratum and are not 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. The biotope is found in wave sheltered to extremely sheltered habitats. In these locations, the breadcrumb sponge *Halichondria panicea* grows in massive forms. Poorly attached massive forms may be ripped off by an increase in water flow rate leading to the death of large colonies. A reduction in wave action would have little effect as the species is naturally found in wave sheltered conditions.

Sensitivity assessment. *Fucus serratus* and associated communities are sensitive to an increase in wave action as increased exposure would result in important losses both in biomass and species richness. The biotope may be preplaced by another *Fucus serratus* dominated biotope e.g. LR.MLR.BF.Fser. Resistance is thus assessed as 'Medium'. Recovery will depend on the extent of *Fucus serratus* loss but will be rapid once conditions return to normal if some of population remain, resulting in 'High' resilience. Overall this biotope group scores a 'Low' sensitivity to this pressure at the pressure benchmark.

Chemical Pressures

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

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

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

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

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

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

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

No evidence

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

This pressure is **Not assessed**.

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

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). Josefson & Widbom (1988) investigated the response of benthic macro and meiofauna to reduced dissolved oxygen levels in the bottom waters of a fjord in Sweden. 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.

Sensitivity assessment. Macroalgae are 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 strong water movement in tide-swept tidal currents combined with turbulent flow over rocks would aerate the water column, and emersion at low tide would mean that any oxygen depletion was transient. 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: Low C: Medium	Not sensitive Q: High A: Low C: Medium

Nutrient enrichment generally stimulates ephemeral macroalgae growth (Duarte, 1995). This stimulation of annual ephemerals may accentuate the competition for light and space and hinder perennial species development or harm their recruitment (Kraufvelin *et al*., 2007). Krauflin *et al.* (2006) found only minor effects on the fucoid community structure as a response to high nutrient levels during the first 3 years of the experiment. During the 4th year of exposure, however, *Fucus serratus* started to decline and population consequently crashed in the 5th year. The study observed full recovery of the algal canopy and animal community in less than two years after conditions returned to normal. The results indicate that established rocky shore communities of perennial algae with associated fauna are able to persist for several years, even at very high nutrient levels, but that community shifts may suddenly occur if eutrophication continues. They also indicate that rocky shore communities have the ability to return rapidly to natural undisturbed conditions after the termination of nutrient enhancement.

An influx of nutrients is also likely to stimulate phytoplankton production, depending on other environmental conditions. This means that the amount of food potentially available to the suspension feeders could increase but in the long-term, a sustained increase in nutrients could lead to algal blooms. Algal blooms have the potential to block light from underlying plants, thereby reducing their photosynthetic capacity. In addition, the eventual biodegradation of the blooms will result in the reduction of available oxygen causing reduced growth in macroalgae species such as *Fucus serratus.* Johansson *et al.* (1998) investigated the changes in the algal vegetation of the Swedish Skagerrak coast, an area heavily affected by eutrophication, between 1960 and 1997. Slow growing species, including *Chondrus crispus,* declined in abundance, probably due to competition from faster growing red algal species such as *Phycodrys rubens* and *Delesseria sanguinea.* However, this biotope occurs in areas with moderately strong to very strong tidal currents rapidly renewing depleted oxygen levels ('see 'de-oxygenation' pressure).

Sensitivity assessment. The benchmark of this pressure (compliance with WFD 'good' status) allows for a slightly less diverse community of red, green and brown seaweeds with cover variable depending on local physical conditions. Therefore, at the level of the benchmark both resistance and resilience are assessed as 'High'. The biotope group is, therefore 'Not Sensitive' to this pressure at the pressure benchmark.

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

Organic enrichment can stimulate the production of primary consumers and may lead to eutrophication (see 'nutrient enrichment' pressure). Husa *et al.* (2014) found that the macroalgal communities beyond the immediate proximity of fish farms in Hardangerfjord, Norway, seemed to be little affected by the deposition of organic matter from the salmon farming industry. Bellgrove *et al.* (2010) however determined that coralline turfs out-competed fucoids at a site associated with organic enrichment caused by an ocean sewage outfall.

Sensitivity assessment. At the level of the benchmark, resistance is assessed as 'Medium' as some mortalities are likely to occur. Recovery will be rapid resulting in 'High' resilience score. The biotope has thus a 'Low' sensitivity to organic enrichment at the level of the benchmark.

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

This biotope group occurs on hard substratum (bedrock, boulders, pebbles and cobbles). A change towards a sedimentary or soft rock substratum would lead to the direct loss of suitable attachment areas resulting in the loss of *Fucus serratus*, *Chondrus crispus* and other red seaweeds. The loss of macroalgae will result in the loss of habitat for associated sponge and ascidian communities. Resistance is assessed as 'Low'. As this pressure represents a permanent change, recovery is impossible as the suitable substratum for fucoids is lacking. Consequently, resilience is assessed as 'Very low' (the pressure is a permanent change). The habitat, therefore, scores a 'High' sensitivity. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

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

Not relevant to biotopes found on hard rock substratum.

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

Extraction of substratum is considered unlikely and this pressure is considered to be 'Not relevant' to hard substratum habitats.

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

The biotope group is found in the lower intertidal, an area easily accessible by humans, especially at low tide. Most macroalgae are very flexible but not physically robust. The trampling of shores by humans will result in increased breakage of algal thalli, decreased thallus height and a net reduction in biomass (see Tyler-Walters & Arnold, 2005 for review).

In the UK, Boalch *et al.* (1974) and Boalch & Jephson (1981) noted a reduction in the cover of fucoids at Wembury, south Devon, when compared to surveys conducted by Colman (1933). The size ranges of *Ascophyllum nodosum*, *Fucus vesiculosus* and *Fucus serratus* were skewed to a smaller length, and the abundance of *Ascophyllum nodosum*, in particular, was reduced (Boalch & Jephson, 1981). It was suggested that visitor pressure, especially after the construction of a car park, was responsible for the reduced cover of fucoids (Boalch *et al.*, 1974). They suggested that the raised edges of the slatey rock severed fronds when the rocks were walked over. However, no quantitative data was provided.

Pinn & Rodgers (2005) compared a heavily visited ledge with a less visited ledge at Kimmeridge Bay, Dorset. Although the mean species richness was similar at both sites, the total number of species was greater at the less utilized site. Comparatively, the heavily utilized ledge displayed a reduction in larger, branching algal species (e.g. *Fucus serratus*) and increased abundances of ephemeral and crustose species (e.g. *Ulva linza* and *Lithothamnia* spp. respectively). Fletcher and

Frid (1996a; 1996b) examined the effects of persistent trampling on two sites on the north-east coast of England. The trampling treatments used were 0, 20, 80, and 160 steps per m^2 per spring tide for 8 months between March and November. Using multivariate analysis, they noted that changes in the community dominated by fucoids (*Fucus vesiculosus*, *Fucus spiralis* and *Fucus serratus*) could be detected within 1 to 4 months of trampling, depending on intensity. Intensive trampling (160 steps/m^2 /spring tide) resulted in a decrease in species richness at one site. The area of bare substratum also increased within the first two months of trampling but declined afterwards, although bare space was consistently most abundant in plots subject to the greatest trampling (Fletcher & Frid, 1996a, 1996b). The abundance of fucoids was consistently lower in trampled plots than in untrampled plots. Fletcher and Frid (1996a) noted that the species composition of the algal community was changed by as little as 20 steps per m^2 per spring tide of continuous trampling since recolonization could not occur. A trampling intensity of 20 steps per m^2 per spring tide could be exceeded by only five visitors taking the same route out and back again across the rocky shore in each spring tide. Both of the sites studied receive hundreds of visitors per year and damage is generally visible as existing pathways, which are sustained by continuous use (Fletcher & Frid, 1996a, 1996b). However, the impact was greatest at the site with the lower original abundance of fucoids.

Brosnan & Crumrine (1994) noted that trampling significantly reduced algal cover within 1 month of trampling. Foliose algae were particularly affected and decreased in cover from 75% to 9.1% in trampled plots. *Mastocarpus papillatus* decreased in abundance from 9% to 1% in trampled plots but increased in control plots. *Fucus distichus* decreased in the summer months only to recover in winter but in trampled plots remained in low abundance (between 1 and 3% cover). Trampling resulted in a decrease in the cover of *Pelvetiopsis limitata* from 16% to 1.5%. *Iridaea cornucopiae* decreased from 38 to 14% cover within a month and continued to decline to 4-8% cover. However, after trampling ceased, recovery of algal cover including *Iridaea cornucopiae* and *Mastocarpus papillatus* was rapid (ca 12 months) (Brosnan & Crumrine, 1994). Fletcher & Frid (1996a; 1996b) reported a decrease in the understory algal community of encrusting coralline algae and red algae, which was probably an indirect effect due to increased desiccation after removal of the normally protective fucoid canopy (see Hawkins & Harkin, 1985) by trampling. They also noted that opportunistic algae (e.g. *Ulva* sp.) increased in abundance. Schiel & Taylor (1999) also observed a decrease in understorey algae (erect and encrusting corallines) after 25 or more tramples, probably due to an indirect effect of increased desiccation as above. However, Schiel & Taylor (1999) did not detect any variation in other algal species due to trampling effects. Similarly, Keough & Quinn (1998) did not detect any effect of trampling on algal turf species.

Algal turfs seem to be relatively tolerant of the direct effects of trampling (based on the available evidence) and some species may benefit from the removal of canopy forming algae (Tyler-Walters, 2005). Their tolerance may result from their growth form as has been shown for vascular plants and corals (Liddle, 1997). Brosnan (1993) suggested that algal turf dominated areas (on shores usually dominated by fucoids) were indicative of trampling on the rocky shores of Oregon. However, tolerance is likely to vary with species and their growth form and little species specific data was found. Furthermore, algal turfs may suffer negative indirect effects where they form an understorey below canopy forming species.

Conversely, fucoid algae are particularly intolerant of trampling, depending on intensity. Fucoid algae demonstrate a rapid (days to months) detrimental response to the effects of trampling, depending on species, which has been attributed to either the breakage of their fronds across rock surfaces (Boalch *et al.*, 1974) or their possession of small discoid holdfasts that offer little resistance to repeated impacts (Brosnan & Crumrine, 1992; Fletcher & Frid, 1996b). Foliose species such as *Mastocarpus papillatus*, *Pelvetiopsis limitata* and *Iridaea cornucopiae* are also likely to be intolerant of trampling (Brosnan & Crumrine, 1994). Brosnan (1993) suggested that the presence or absence of foliose algae (e.g. fucoids) could be used to indicate the level of trampling on the rocky shores of Oregon.

Once *Fucus serratus* has been removed, understory algae will become exposed. Macroalgae canopies buffer the effects of high temperatures and water loss on organisms below their fronds in particular when exposed to air. For instance Bertness *et al*. (1999) determined that substratum temperatures were on average 8-10°C lower under the canopy than on bare rock. Desiccation of understorey algae will create bare patches (see 'changes in emergence regime' pressure). These bare patches can lead to invasions by grazing limpets which in turn can promote even greater changes in community composition (Little *et al*., 2009). The removal of macroalgae canopy due to abrasion will thus have a direct impact on the entire community. However, cracks and crevices are ideal places for germlings to develop and sessile species to settle as these sites may be protected from abrasion. Stagnol *et al.* (2013) found that opportunistic ephemeral green algae such as *Ulva* sp. responded positively to disturbance. These green ephemeral algae are major competitors of *Fucus serratus* for space colonization and nutrient uptake. Blooms of ephemeral algae facilitated by disturbance may then slow the development of longer-lived perennial algae, especially fucoids. Disturbance is a structuring factor in intertidal habitats. Perturbation events often remove organisms, increase mortality, and release resources such as space, nutrients and light that may enhance the appearance of new colonists (Connell *et al.*, 1997). As a result of these contrasting effects, post-disturbance communities are frequently different from initial communities in terms of composition and dominance of species. Overall, disturbance causes a shift towards a disturbance tolerant seaweed community (Little *et al.*, 2009).

Epifaunal species have been found to be particularly adversely affected by physical disturbance, either due to direct damage or modification of the habitat (Jennings & Kaiser, 1998). Similarly, Dayton (1971) observed greatly reduced the abundance of species living on, under, and among fucoids following large disturbance events. Hydroids, bryozoans and encrusting fauna are easily ripped from the substratum and are unlikely to re-attach and will die. The shells of limpets, tubeworms and periwinkles may be crushed by the weight and force of the abrasion. However, some epifaunal species have been reported to exhibit increased abundances on high fishing effort areas, probably due to their ability to colonize and grow rapidly (Bradshaw *et al*., 2000). For instance, *Ascidiella* species had increased in abundance in an area subject to scallop dredging (Bradshaw *et al*., 2002). The breadcrumb sponge *Halichondria panicea* is attached to the substratum and will not survive abrasion and physical disturbance. Hiscock (1983) noted that a community, under conditions of scour and abrasion from stones and boulders moved by storms, developed into a community consisting of fast growing species such as *Spirobranchus triqueter* due to decreased competition. A shift in community composition is thus expected immediately after the disturbance event.

The effects of trampling are dependent on intensity, expressed as frequency and force per unit area of the impacting 'foot print' (see Liddle, 1997, Tyler-Walters & Arnold, 2008). Clearly, mechanical abrasion due to vehicles, jack-up-barges, or grounding vessels will exceed the abrasive 'intensity' of trampling by humans or livestock.

Sensitivity assessment. Physical disturbance resulting from activities such as trampling (by humans and livestock) or abrasive activities (e.g. vehicles, jack-up-barges, or grounding vessels) could cause a significant loss of fucoid cover and an important reduction in species abundance and diversity. Resistance is thus assessed as 'Low'. If some *Fucus serratus* population remain recovery will be fair. However, recruitment mortality, grazing by limpets and the presence of turfs and encrusting algae can slow down and limit recovery. Resilience is thus assessed as 'Medium'. The biotope, therefore, scores a 'Medium' sensitivity to abrasion pressure. If the entire population of *Fucus serratus* is removed, other species may come to dominate and the recovery will take considerably longer. Re-establishment of the seaweed may depend on the ability to out-compete other species and this may be dependent on suitable environmental conditions.

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	High Q: High A: Low C: Medium	Low Q: Medium A: Low C: Medium

Light is an essential resource for all photoautotrophic organisms. Changes in suspended solids affecting water clarity will have a direct impact on the photosynthesising capabilities of *Fucus serratus*. Irradiance below light compensation point of photosynthetic species can compromise carbon accumulation (Middelboe *et al*., 2006). However, water clarity is only relevant when the biotope is covered with water. Seaweed photosynthesis declines on emersion and recommences when recovered with water. In addition, increased siltation may cover the frond surface of *Fucus serratus* 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 (see 'siltation' pressures). Red algae can tolerate a wider range of light levels than any other group of photosynthetic plants (Kain & Norton, 1990) and will, therefore, be less affected by a reduction in water clarity.

In turbid waters, the feeding apparatus of suspension feeders may become clogged with particles interfering with their feeding and respiratory currents resulting in net losses. For instance, the hydroid *Dynamena pumila* experienced marked decline in areas with increased silt content in Strangford Lough, Northern Ireland (Seed *et al*., 1983). Some filter feeders have the ability to cope with siltation and excess suspended material. For example, the sea squirt *Ascidiella scabra* can extend its siphons to a small extent and can maintain a passage through the silt to the siphons. However, Robbins (1985b) found that increased inorganic particulate concentrations reduced growth rates of *Ascidiella scabra* with mortalities occurring in a high level of suspended sediments. The breadcrumb sponge *Halichondria panicea* has a cleaning mechanism sloughing off its complete outer tissue layer together with any debris (Barthel & Wolfrath, 1989). There is, however, an energetic cost in cleaning resulting in reduced growth. For short-lived species, such as the star ascidian *Botryllus schlosseri*, reduced growth could prove fatal.

Sensitivity assessment. Changes in suspended solids reducing water clarity will have adverse effects on the biotope group reducing species richness. Resistance is thus assessed as 'Medium'. Once conditions return to 'normal' *Fucus serratus* is likely to rapidly regain photosynthesising capabilities as well as growth rate. Associated communities will also rapidly 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 thus assessed as ‘High’. Overall this biotope group scores a ‘Low’ sensitivity to this pressure.

Smothering and siltation rate changes (light)	High Q: High A: Medium C: Medium	High Q: Medium A: Medium C: Medium	Not sensitive Q: Medium A: Medium C: Medium

Macroalgae are attached to the substratum by a holdfast and are thus not able to relocate in response to increased sedimentation. Sedimentation of bedrock can impede attachment of *Fucus* embryos as well as decrease survival and growth of juvenile through both scour and burial (Schiel *et al*., 2006). An increase in the vertical sediment overburden can also reduce growth whilst hindering the regeneration abilities of adults (Umar *et al*., 1998).

Some filter feeders have the ability to cope with siltation and excess suspended material. For example, *Ascidiella scabra* can extend its siphons, to a small extent, above silt whilst maintaining a passage through the silt to the siphons. It also attaches to other erect biota and may thereby escape smothering effects. The breadcrumb sponge *Halichondria panicea* has a mechanism for sloughing off its complete outer tissue layer together with any debris (Barthel & Wolfrath, 1989). However, there is an energetic cost in cleaning, and this species, together with other filter feeders, would probably experience reduced. For annual species, including the star ascidian *Botryllus schlosseri*, reduced growth could prove fatal. The hydroid *Dynamena pumila* experienced marked decline in areas with increased silt content in Strangford Lough, Northern Ireland (Seed *et al*., 1983).

Sensitivity assessment. Smothering by a 5 cm layer of sediment is unlikely to adversely affect this biotope given that it is associated with areas of moderately strong to very strong tidal flow. The sediment layer will be washed away and 'normal' conditions will resume rapidly. The suspension feeders may experience some short-lived interference with feeding but, at the level of the benchmark, this is not likely to adversely affect their viability. Resistance and resilience are therefore both assessed as ‘High’ (no impacts to recover from). The biotope group is ‘Not Sensitive’ to a decrease in salinity at the pressure benchmark.

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

Several studies found that increasing the vertical sediment burden negatively impact species characterizing this biotope. At the level of the benchmark (30 cm of fine material added to the seabed in a single event), smothering will result in important mortalities. Resistance is assessed as ‘Low’ as all individuals exposed to siltation at the benchmark level are predicted to die. However, the biotope is associated with areas of moderately strong to very strong tidal flow. The sediment layer will be washed away and 'normal' conditions will resume rapidly. Resilience is thus assessed as ‘Low’ and resistance as ‘Medium. Sensitivity based on combined resistance and resilience is therefore assessed as ‘Medium’.

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

Not assessed.

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

Not relevant

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

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

Introduction of light or shading	Medium Q: High A: Low C: High	High Q: High A: Medium C: Medium	Low Q: High A: Low C: Medium

Fucoids are dependent on light so that changes in light intensity are likely to affect photosynthesis, growth, competition and survival. Chapman (1995) noted that too little or too much light are likely to be stresses. There is considerable literature on the light compensation point of marine algae (see Luning, 1990) but it is difficult to correlate such evidence with 'shading', as light saturation and compensation points depend on light availability, light quality, season and turbidity. As fucoids are out-competed in sublittoral conditions, it is likely that permanent shading would affect their growth and allow them to be out-competed by other, more shade tolerant species, within the affected area. Therefore a resistance of ' Medium' is suggested albeit at low confidence. Resilience is likely to be 'High' so that sensitivity is 'Low.

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

Biological Pressures

	Resistance	Resilience	Sensitivity

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

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

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

Thompson & Schiel (2012) found that native fucoids showed high resistance to invasions by the Japanese kelp *Undaria pinnatifida*. However cover of *Fucus serratus* was inversely correlated with the cover of *Sargassum muticum* indicating competitive interaction between the two species (Stæhr *et al*., 2000). Stæhr *et al*. (2000) determined that the invasion of *Sargassum muticum* could affect local algal communities through competition mainly for light and space. The Portuguese oyster *Magallana gigas* was introduced in England in 1926 for cultivation purposes and is now found in the wild. The species can form dense beds e.g. in the Netherlands, and, together with *Crepidula fornicata*, have the potential to cover large patches on the shore. In areas where the biotope coincides with the distribution of *Magallana gigas*, i.e. the south coast of Devon and coast of Essex, the oyster may become dominant.

Sensitivity assessment. Resistance is assessed as 'Medium' since invasive species have the potential to alter the recognizable biotope. Recovery would be rapid once conditions return to normal, resulting in a 'High' resilience. However, return to 'normal' conditions is highly unlikely if an invasive species would come to dominate the biotope. Indeed recovery would only be possible if the majority of the INIS were removed (through either natural or unnatural process) to allow the re-establishment of other species. Therefore actual resilience will be much lower ('Low' to 'Very Low') resulting in an overall 'Medium' sensitivity score.

Introduction of microbial pathogens	High Q: Low A: NR C: NR	High Q: Low A: NR C: NR	Not sensitive Q: Low A: NR C: NR

Very little is known about infections in *Fucus* (Wahl *et al*., 2012). Coles (1958) identified parasitic nematodes that caused galls on *Fucus serratus* in the Southwest of Britain. More recently, Zuccaro *et al*. (2008) detected a number of fungal species associated with *Fucus serratus*. So far no mortalities have been associated to the introduction of microbial pathogens however the potential for increased biotic interactions involving parasites or pathogens is on the rise in many marine systems (Torchin *et al*., 2002). Other characteristic species, for example *Chondrus crispus* and *Mytilus edulis* are known to be adversely affected by infestation by microbial pathogens (see relevant MarLIN reviews). However, even if microbial infestation resulted in the loss of these two species from the biotope, the recognizable biotope per se would not be affected.

Sensitivity assessment. Both resistance and resilience are assessed as 'High'; the biotope is therefore 'Not Sensitive' to this pressure. However the assessment has a low confidence score as more research is needed into the effects of microbial pathogen on *Fucus serratus* and associated communities.

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

Fucus serratus is one of several harvested and exploited algal species. Seaweeds were collected from the middle of the 16th century for the iodine industry. Nowadays seaweeds are harvested for their alginates, which are used in the cosmetic and pharmaceutical industries, for agricultural supply, water treatment, and for human food and health supplements (Bixler & Porse, 2010).

The commercial harvest removes seaweed canopies which will have important direct and indirect effects on the wider ecosystem. Stagnol et al.(2013) investigated the effects of commercial harvesting of intertidal Fucus serratus on ecosystem biodiversity and functioning. The study found that the the removal of macroalgae 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; Golléty *et al.*, 2008). Removal of the canopy caused bleaching and death of understorey red turfing algae. 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 Fucus serratus on the impact zone. Due to the high intolerance of macroalgae communities to human exploitation, the European Union put in place a framework to regulate the exploitation of algae establishing an organic label that implies that 'harvest shall not cause any impact on ecosystems' (no. 710/2009 and 834/2007).

Sensitivity assessment. Removal of the *Fucus serratus* canopy will have a negative impact on the diversity of animal community and the metabolism of the area. The harvesting impact on the animal community was amplified by the settlement of an ephemeral canopy of *Ulva* spp., a seasonal opportunistic green alga (Stagnol *et al.*,2013). Resistance is thus assessed as 'Low'. If some *Fucus serratus* population remain recovery will be fairly rapid. However recruitment mortality, grazing by limpets and the presence of turfs and encrusting algae can slow down and limit recovery. A switch to a disturbance community will also slow the recovery of Fucus serratus and associated community. Resilience is thus assessed as 'Medium'. The biotope therefore scores a 'Medium' sensitivity to this pressure. If the entire population of *Fucus serratus* is removed, other species may come to dominate and the recovery will take considerably longer. Re-establishment of the seaweed may depend on the ability to out-compete other species and this may be dependent on suitable environmental conditions.

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

The harvest of algae, crabs snails, mussels, and some species of fish from the shore is a widespread practice. None of the components of this biotope have known obligate relationships and the removal of non-target species will therefore not have a significant impact. Resistance to this pressure is deemed 'High'. Resilience is also 'High' as there are no ecological impacts to recover from, resulting in a ‘Not Sensitive’ score. The assessment is based on expert knowledge resulting in a 'Low' confidence score.

Components of this biotope may be directly removed or damaged by static or mobile gears that are targeting other species. These direct, physical impacts are assessed through the abrasion and penetration of the seabed pressures. The sensitivity assessment for this pressure considers any biological/ecological effects resulting from the removal of non-target species on this biotope.

Bibliography

Airoldi, L., Balata, D. & Beck, M.W., 2008. The Gray Zone: relationships between habitat loss and marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology*, **366** (1), 8-15.

Arrontes, J., 1993. Nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. *Marine Ecology Progress Series*, **93**, 183-183.

Arrontes, J., 2002. Mechanisms of range expansion in the intertidal brown alga *Fucus serratus* in northern Spain. *Marine Biology*, **141** (6), 1059-1067.

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

Beer, S., Björk, M. & Beardall, J., 2014. *Photosynthesis in the Marine Environment.* John Wiley & Sons.

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

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R. & Ingraham, A.O., 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology*, **80** (8), 2711-27

Bertocci, I., Arenas, F., Matias, M., Vaselli, S., Araújo, R., Abreu, H., Pereira, R., Vieira, R. & Sousa-Pinto, I., 2010. Canopy-forming species mediate the effects of disturbance on macroalgal assemblages on Portuguese rocky shores. *Marine Ecology Progress Series*, **414**, 107-116.

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

Boaden, P.J.S., O' Connor, R.J. & Seed, R., 1975. The composition and zonation of a *Fucus serratus* community in Strangford Lough, Co. Down. *Journal of Experimental Marine Biology and Ecology*, **17**, 111-136.

Boalch, G.T. & Jephson, N.A., 1981. A re-examination of the seaweeds on Colman's traverses at Wembury. *Proceedings of the International Seaweed Symposium*, **8**, 290-293.

Boalch, G.T., Holme, N.A., Jephson, N.A. & Sidwell, J.M.C., 1974. A resurvey of Colman's intertidal traverses at Wembury, South Devon. *Journal of the Marine Biological Association of the United Kingdom*, **5**, 551-553.

Bokn, T.L., Moy, F.E. & Murray, S.N., 1993. Long-term effects of the water-accommodated fraction (WAF) of diesel oil on rocky shore populations maintained in experimental mesocosms. *Botanica Marina*, **36**, 313-319.

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

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

Brawley, S.H., 1992a. Fertilization in natural populations of the dioecious brown alga *Fucus ceranoides* and the importance of the polyspermy block. *Marine Biology*, **113** (1), 145-157.

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

Brawley, S.H., Coyer, J.A., Blakeslee, A.M., Hoarau, G., Johnson, L.E., Byers, J.E., Stam, W.T. & Olsen, J.L., 2009. Historical invasions of the intertidal zone of Atlantic North America associated with distinctive patterns of trade and emigration. *Proceedings of the National Academy of Sciences*, **106** (20), 8239-8244.

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., 1992. Human impact and a management strategy for Yaquina Head Outstanding Natural Area (summary only). A report to the Bureau of Land Management, Department of the Interior, Salem, Oregon.

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.

Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F. & Hawkins, S.J., 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **267** (1), 89-106.

Castric-Fey, A., 1983. Recruitment, growth and longevity of *Pomatoceros triqueter* and *Pomatoceros lamarckii* (Polychaeta, Serpulidae) on experimental panels in the Concarneau area, South Brittany. *Annales de l'Institut Oceanographique, Paris*, **59**, 69-91.

Chapman, A.R.O. (1995). Functional ecology of fucoid algae: twenty-three years of progress. *Phycologia*, **34**(1), 1-32.

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., Hughes, T.P. & Wallace, C.C., 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs*, **67** (4), 461-488.

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/

Coyer, J., Hoarau, G., Skage, M., Stam, W. & Olsen, J., 2006a. Origin of *Fucus serratus* (Heterokontophyta; Fucaceae) populations in Iceland and the Faroes: a microsatellite-based assessment. *European Journal of Phycology*, **41** (2), 235-246.

Coyer, J., Peters, A., Stam, W. & Olsen, J., 2003. Post-ice age recolonization and differentiation of *Fucus serratus* L. (Phaeophyceae; Fucaceae) populations in Northern Europe. *Molecular Ecology*, **12** (7), 1817-1829.

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

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, **41** (4), 351-389.

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

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

Dons, C., 1927. Om Vest og voskmåte hos *Pomatoceros triqueter*. *Nyt Magazin for Naturvidenskaberne*, **LXV**, 111-126.

Duarte, C.M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia*, **41** (1), 87-112.

Dudgeon, S.R. & Johnson, A.S., 1992. Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgement of two co-dominant seaweeds . *Journal of Experimental Marine Biology and Ecology*, **165**, 23-43.

Dudgeon, S.R., Steneck, R.S., Davison, I.R. & Vadas, R.L., 1999. Coexistence of similar species in a space-limited intertidal zone. *Ecological Monographs*, **69**, 331-352.

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

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

Fletcher, H. & Frid, C.L.J., 1996b. The response of an inter-tidal algal community to persistent trampling and the implications for rocky shore management. In Jones, P.S., Healy, M.G. & Williams, A.T. (ed.) Studies in European coastal management., Cardigan, Wales: Samara Publishing

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.

Fretter, V. & Graham, A., 1994. *British prosobranch molluscs: their functional anatomy and ecology*, revised and updated edition. London: The Ray Society.

Gili, J-M. & Hughes, R.G., 1995. The ecology of marine benthic hydroids. *Oceanography and Marine Biology: an Annual Review*, **33**, 351-426.

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.

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

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.

Hawkins, S.J. & Harkin, E., 1985. Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. *Botanica Marina*, **28**, 223-30.

Hawkins, S.J. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265-271.

Hawkins, S.J. & Southward, A.J., 1992. The *Torrey Canyon* oil spill: recovery of rocky shore communities. In *Restoring the Nations Marine Environment, (ed. G.W. Thorpe), Chapter 13, pp. 583-631.* Maryland, USA: Maryland Sea Grant College.

Hayward, P.J. & Ryland, J.S. (ed.) 1995a. *The marine fauna of the British Isles and north-west Europe. Volume 2. Molluscs to Chordates.* Oxford Science Publications. Oxford: Clarendon Press.

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).

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

Hoarau, G., Coyer, J., Veldsink, J., Stam, W. & Olsen, J., 2007. Glacial refugia and recolonization pathways in the brown seaweed *Fucus serratus. Molecular Ecology*, **16** (17), 3606-3616.

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

Husa, V., Kutti, T., Ervik, A., Sjøtun, K., Hansen, P.K. & Aure, J., 2014. Regional impact from fin-fish farming in an intensive production area (Hardangerfjord, Norway). *Marine Biology Research*, **10** (3), 241-252.

Jenkins, C., Haas, M., Olson, A. & Ruesink, J., 2002. Impacts of trampling on a rocky shoreline of San Juan Island, Washington, USA. *Natural Areas Journal*, **22** (4), 260-269.

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.

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

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

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

Johansson ,G., Eriksson, B.K., Pedersen, M. & Snoeijs, P., 1998. Long term changes of macroalgal vegetation in the Skagerrak area. *Hydrobiologia*, **385**, 121-138.

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

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.

Jueterbock, A., Kollias, S., Smolina, I., Fernandes, J.M., Coyer, J.A., Olsen, J.L. & Hoarau, G., 2014. Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: Acclimatization potential to climate change. *Marine Genomics*, 13, 27-36.

Kain, J.M., & Norton, T.A., 1990. Marine Ecology. In *Biology of the Red Algae*, (ed. K.M. Cole & Sheath, R.G.). Cambridge: Cambridge University Press.

Keough, M.J. & Quinn, G.P., 1998. Effects of periodic disturbances from trampling on rocky intertidal algal beds. *Ecological Applications*, **8** (1), 141-161.

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

Knowlton, A.L. & Highsmith, R.C., 2005. Nudibranch-sponge feeding dynamics: Benefits of symbiont-containing sponge to Archidoris montereyensis (Cooper, 1862) and recovery of nudibranch feeding scars by *Halichondria panicea* (Pallas, 1766). *Journal of Experimental Marine Biology and Ecology*, **327** (1), 36-46.

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

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

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

Liddle, M.J., 1997. *Recreational ecology. The ecological impact of outdoor recreation and ecotourism.* London: Chapman & Hall.

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., Partridge, J.C. & Teagle, L., 1991. Foraging activity of limpets in normal and abnormal tidal regimes. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 537-554.

Little, C., Williams, G.A. & Trowbridge, C.D., 2009. *The biology of rocky shores*: Oxford University Press New York.

Lüning, K., 1984. Temperature tolerance and biogeography of seaweeds: the marine algal flora of Helgoland (North Sea) as an example. *Helgolander Meeresuntersuchungen*, **38**, 305-317.

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.

Mangialajo, L., Chiantore, M. & Cattaneo-Vietti, R., 2008. Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. *Marine Ecology Progress Series*, **358**, 63.

Martínez, B., Arenas, F., Rubal, M., Burgués, S., Esteban, R., García-Plazaola, I., Figueroa, F., Pereira, R., Saldaña, L. & Sousa-Pinto, I., 2012. Physical factors driving intertidal macroalgae distribution: physiological stress of a dominant fucoid at its southern limit. *Oecologia*, **170** (2), 341-353.

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

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.

Moore, H.B., 1937. *Marine Fauna of the Isle of Man.* Liverpool University Press.

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

Nielsen, S.L., Nielsen, H.D. & Pedersen, M.F., 2014. Juvenile life stages of the brown alga *Fucus serratus* L. are more sensitive to combined stress from high copper concentration and temperature than adults. *Marine Biology*, **161** (8), 1895-1904.

Norton, T.A., 1992. Dispersal by macroalgae. *British Phycological Journal*, **27**, 293-301.

Nygård, C.A. & Dring, M.J., 2008. Influence of salinity, temperature, dissolved inorganic carbon and nutrient concentration on the photosynthesis and growth of *Fucus vesiculosus* from the Baltic and Irish Seas. *European Journal of Phycology*, **43** (3), 253-262.

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

Orlov, D.V., 1996. The role of larval settling behaviour in determination of the specific habitat of the hydrozoan *Dynamena pumila* (L.). Larval settlement in *Dynamena pumila* (L.). *Journal of Experimental Marine Biology and Ecology*, **208**, 73-85.

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.

Perkol-Finkel, S. & Airoldi, L., 2010. Loss and recovery potential of marine habitats: an experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. *PLoS One*, **5** (5), e10791.

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.

Price, J.H., Irvine, D.E. & Farnham, W.F., 1980. *The shore environment. Volume 2: Ecosystems.* London Academic Press.

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

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

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

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

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

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

Schiel, D.R. & Lilley, S.A., 2011. Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. *Journal of Experimental Marine Biology and Ecology*, **407** (1), 108-115.

Schiel, D.R. & Taylor, D.I., 1999. Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. *Journal of Experimental Marine Biology and Ecology*, **235**, 213-235.

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.

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

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

Seed, R., 1985. Ecological pattern in the epifaunal communities of coastal macroalgae. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.* (ed. P.G. Moore & R. Seed), pp. 22-35. London: Hodder & Stoughton Ltd.

Seed, R., Elliott, M.N., Boaden, P.J.S. & O' Connor, R.J.O., 1981. The composition and seasonal changes amongst the epifauna associated with *Fucus serratus* L. in Strangford Lough, Northern Ireland. *Cahiers de Biologie Marine*, **22**, 243-266.

Seed, R., O'Connor, R.J. & Boaden, P.J.S., 1983. The spatial niche of *Dynamena pumila* (L.) and *Gonothyraea loveni* (Allman) (Hydrozoa) within a *Fucus serratus* L. community. *Cahiers de Biologie Marine*, **24**, 391-419.

Segrove, F., 1941. The development of the serpulid *Pomatoceros triqueta L. Quarterly Journal of Microscopical Science*, **82**, 467-540.

Serrão, E.A., Brawley, S.H., Hedman, J., Kautsky, L. & Samuelsson, G., 1999. Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Journal of Phycology*, **35** (2), 254-269.

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

Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T. & Krause-Jensen, D., 2000. Invasion of *Sargassum muticum* in Limfjorden

(Denmark) and its possible impact on the indigenous macroalgal community. *Marine Ecology Progress Series*, **207**, 79-88.

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.

Strömgren, T., 1979b. The effect of zinc on the increase in length of five species of intertidal Fucales. *Journal of Experimental Marine Biology and Ecology*, **40**, 95-102.

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

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

Suzuki, N. & Mittler, R., 2006. Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction. *Physiologia Plantarum*, **126** (1), 45-51.

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

Thomas, J.G., 1940. *Pomatoceros*, *Sabella* and *Amphitrite*. LMBC Memoirs on typical British marine plants and animals no.33. University Press of Liverpool. Liverpool

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

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

Tyler-Walters, H., 2005b. Assessment of the potential impacts of coasteering on rocky intertidal habitats in Wales. *Report to Cyngor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN).* Marine Biological Association of the United Kingdom, Plymouth, 129 pp.

Umar, M., McCook, L. & Price, I., 1998. Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. *Coral Reefs*, **17** (2), 169-177.

Viejo, R.M., Martínez, B., Arrontes, J., Astudillo, C. & Hernández, L., 2011. Reproductive patterns in central and marginal populations of a large brown seaweed: drastic changes at the southern range limit. *Ecography*, **34** (1), 75-84.

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.

Wahl, M., Shahnaz, L., Dobretsov, S., Saha, M., Symanowski, F., David, K., Lachnit, T., Vasel, M. & Weinberger, F., 2010. Ecology of antifouling resistance in the bladder wrack *Fucus vesiculosus*: patterns of microfouling and antimicrobial protection. *Marine Ecology Progress Series*, **411**, 33-48.

Zou, D., Liu, S., Du, H. & Xu, J., 2012. Growth and photosynthesis in seedlings of *Hizikia fusiformis* (Harvey) Okamura (Sargassaceae, Phaeophyta) cultured at two different temperatures. *Journal of Applied Phycology*, **24** (5), 1321-1327.

Zuccaro, A., Schoch, C.L., Spatafora, J.W., Kohlmeyer, J., Draeger, S. & Mitchell, J.I., 2008. Detection and identification of fungi intimately associated with the brown seaweed *Fucus serratus*. *Applied and Environmental Microbiology*, **74** (4), 931-941.