



MarLIN

Marine Information Network

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

Mytilus edulis and *Fucus vesiculosus* on moderately exposed mid eulittoral rock

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

Dr Heidi Tillin & Dr Harvey Tyler-Walters

2015-11-03

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/46>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

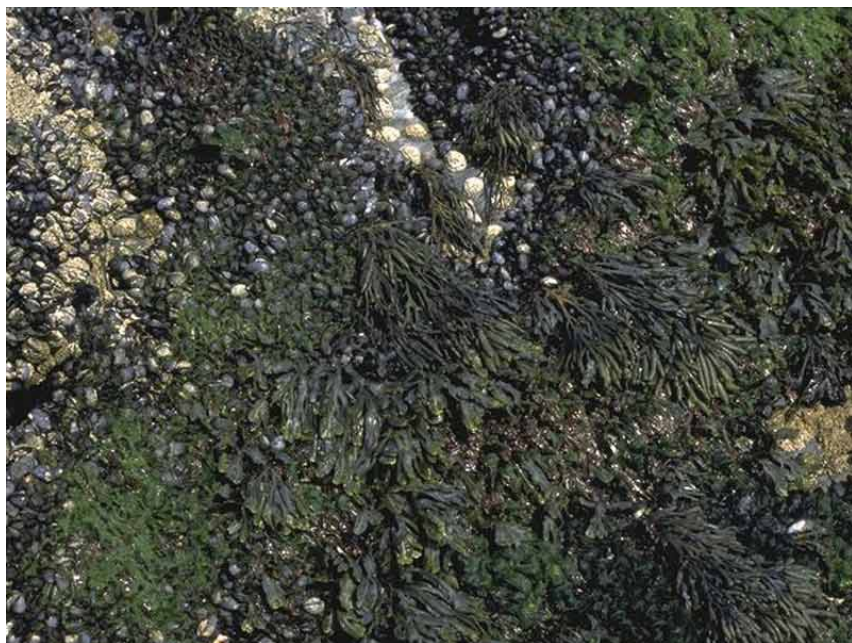
This review can be cited as:

Tillin, H.M. & Tyler-Walters, H., 2015. [*Mytilus edulis*] and [*Fucus vesiculosus*] on moderately exposed mid 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.46.1>



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

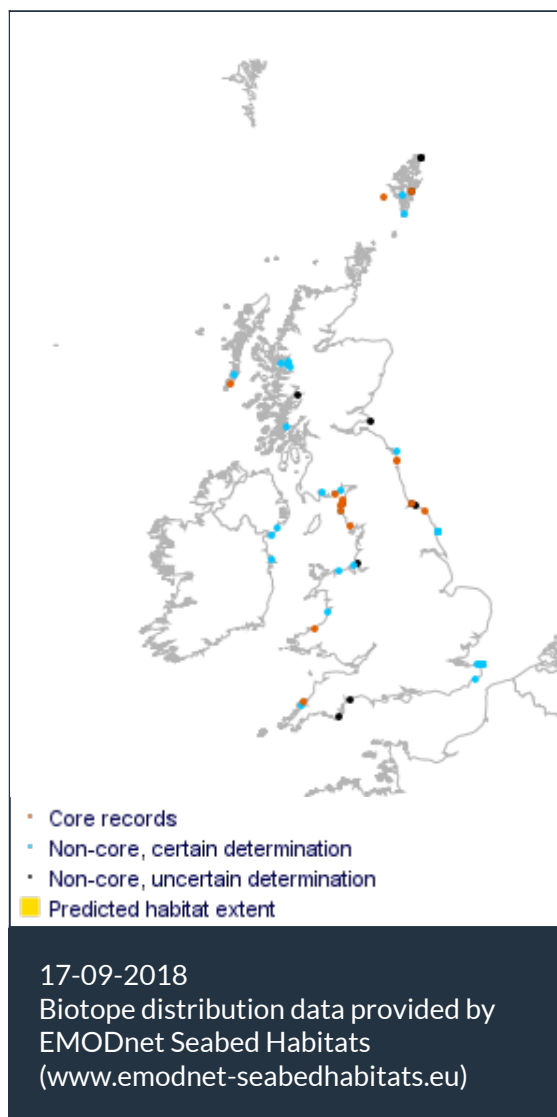
(page left blank)



Mytilus and fucoids.

Photographer: David Connor

Copyright: Joint Nature Conservation Committee (JNCC)



Researched by Dr Heidi Tillin & Dr Harvey Tyler-Walters

Referred by This information is not refereed.

Summary

☰ UK and Ireland classification

EUNIS 2008	A1.221	<i>Mytilus edulis</i> and <i>Fucus vesiculosus</i> on moderately exposed mid eulittoral rock
JNCC 2015	LR.MLR.MusF.MytFves	<i>Mytilus edulis</i> and <i>Fucus vesiculosus</i> on moderately exposed mid eulittoral rock
JNCC 2004	LR.MLR.MusF.MytFves	<i>Mytilus edulis</i> and <i>Fucus vesiculosus</i> on moderately exposed mid eulittoral rock
1997 Biotope	LR.MLR.MF.MytFves	<i>Mytilus edulis</i> and <i>Fucus vesiculosus</i> on moderately exposed mid eulittoral rock

🔍 Description

Mid eulittoral exposed to moderately exposed bedrock, often with nearby sediment, covered by a dense band or large patches of the mussel *Mytilus edulis*. The community often supports scattered

Fucus vesiculosus and occasional foliose red seaweeds such as *Porphyra umbilicalis*, *Osmundea pinnatifida*, *Mastocarpus stellatus*, *Palmaria palmata* or the calcareous algae *Corallina officinalis*. The ephemeral green seaweeds *Ulva intestinalis* and *Ulva lactuca* commonly occur on the shells of the mussels. The barnacle *Semibalanus balanoides* is common on both the mussel valves and on patches of bare rock, where the limpet *Patella vulgata* also can be found. The whelk *Nucella lapillus* and the winkle *Littorina littorea* can be found within the mussel bed (Connor *et al.*, 2004; JNCC).

↓ Depth range

Mid shore

🏛️ Additional information

None entered.

✓ Listed By

- none -

🔗 Further information sources

Search on:



Habitat review

🔄 Ecology

Ecological and functional relationships

The major ecological relationships are between space occupiers and their predators. Space for colonization may be freed by physical factors such as storms or by biological factors such as predation. Ecological relationships important for the function of the community are given below. The following information has been summarised from studies by Suchanek (1985), Tsuchiya & Nishihira (1985 & 1986), Seed & Suchanek (1992) and Holt *et al.* (1998) to which the reader should refer for further details. Please note that recent evidence suggests that the *Mytilus edulis* communities studied by Suchanek 1985 and Tsuchiya & Nishihira (1985, 1986) were probably *Mytilus trossulus* and *Mytilus galloprovincialis* respectively (Seed, 1992), although their community ecology is probably similar.

Competition

- *Mytilus edulis* is a active suspension feeder on phytoplankton, organic particulates and dissolved organic matter, which probably significantly reduces the suspended particulate food (seston) available to other suspension feeders in the biotope.
- Other suspension feeders include the surrounding barnacles, tube worms (e.g. *Spirobranchus* spp.), hydroids (e.g. *Obelia geniculata*), bryozoans (e.g. *Electra pilosa*) and interstitial bivalves such as *Lasaea adansoni*.
- *Mytilus edulis* competes for space with other species such as barnacles and fucoids.
- Where present the biogenic mud under the bed support deposit feeders or detritivores such as polychaetes (e.g. *Cirratulus cirratus* and terebellids).

Predation and herbivory

- The macroalgae (e.g. *Fucus vesiculosus*, *Mastocarpus stellatus*, and *Ceramium* spp.) provide primary production to the community and the surrounding ecosystem directly to grazers, or indirectly in the form of abraded algal particulates and detritus, algal spores, algal exudates and dissolved organic matter.
- The macroalgae support mesoherbivores such as gammarid amphipods and isopods feeding on algal epiphytes and macroalgae (Brawley, 1992b; Tsuchiya & Nishihira, 1985, 1986).
- Epifloral/faunal grazers, such as chitons, limpets, littorinids (e.g. *Littorina littorea*, *Littorina saxatilis*, and *Littorina obtusata*) feed within and around the mussel bed, grazing on benthic microalgae and macroalgae (sporeling and adult plants), and bulldozing newly settled invertebrate larvae (Hawkins & Hartnoll, 1983).
- Grazers have been shown to reduce excessive fouling by epifauna and large macroalgae, and encourage recovery from disturbance in intertidal *Mytilus californianus* populations (Suchanek, 1985; Seed & Suchanek, 1992). This biotope is characterized by the presence of macroalgae and gastropod and mesoherbivore grazing probably prevents the algae and epifauna smothering the mussel bed, although the patches of mussels provide a refuge for the macroalgae from the intense grazing by limpets on the surrounding substratum.
- Predation is the single most important source of mortality in *Mytilus edulis* populations (Seed & Suchanek, 1992; Holt *et al.*, 1998). Many predators target specific sizes of mussels and, therefore influence population size structure. For example, *Carcinus maenas* was

unable to consume mussels of ca. 70mm in length and mussels >45mm long were probably safe from attack (Davies *et al.*, 1980; Holt *et al.*, 1998).

- The lower limit of intertidal mussel populations may be limited by predation by starfish (e.g. *Asterias rubens*), *Carcinus maenas* and the dog whelk *Nucella lapillus*, although dog whelk predation is of more importance in sheltered sites (Holt *et al.*, 1998).
- Flatfish such as *Platichthys flesus* (plaice), *Pleuronectes platessa* (flounder) and *Limanda limanda* (dab), where present, feed on mussels.
- Birds are important predators of mussels, and oystercatchers, herring gulls, eider ducks and knot have been reported to be major sources of *Mytilus edulis* mortality. For example, in the Ythan estuary bird predation accounted for 72% of mussel production, with oystercatchers and herring gulls being each responsible for 15% and mussels are regarded as a staple food of oystercatchers (Dare, 1976; Holt *et al.*, 1998). Although, probably of greatest importance in sedimentary habitats, bird predation, probably significantly affects the population dynamics of intertidal mussel beds.
- Scavengers probably feed on dead mussels within the matrix, e.g. flatworms, small crabs and polychaetes (Kautsky, 1981; Tsuchiya & Nishihira, 1985, 1986), while other polychaetes (e.g. scale worms), small crabs and nemertean and predatory within the matrix.

Seasonal and longer term change

Little season change in the dominant species is likely. *Mytilus edulis* spawns in spring and summer and in some areas again in last August and September, with settlement occurring 1-4 weeks later. However, while recruitment can be annual, it is often sporadic and unpredictable (see below). The species richness of the macro-invertebrate fauna associated with mussel patches was shown to fluctuate seasonally, probably reflecting random fluctuations in settlement and mortality typical of marine species with planktonic larvae (see Seed, 1996 for discussion). Ephemeral green algae may show a peak in abundance during the spring.

Winter storms can result in gaps forming in the mussel bed, especially where the mussels are fouling by macroalgae or epifauna, due to wave action and drag, or direct impact by wave driven debris, e.g. logs (Seed & Suchanek, 1992). Winter storms will also reduce or damage furoids and macroalgal cover (e.g. *Mastocarpus stellatus*). Crab and fish tend to move to deeper water in the winter months, so that predation is probably reduced. Macroalgae probably exhibit minimal cover in winter, growing back in spring and reaching maximum cover in summer. Seed (1996) reported that the invertebrate communities within mussel patches exhibit significant temporal and small-scale spatial variations in diversity and abundance, that probably reflect the stochastic nature of larval recruitment and settlement.

Holt *et al.* (1998) suggested that moderately exposed mussel beds on rock surfaces could be relatively stable and long-lived. In the intertidal, low shore beds probably consist of young individual mussels, due to the intense predation due to starfish and crabs, with few surviving to their second or third year. However, predation pressure decreases with increasing height up the shore, so that mid-shore or high shore populations may consist of a twenty or more year classes, although their growth rates and hence size were much reduced (Seed & Suchanek, 1992). Seed & Suchanek (1992) suggested that although mussel assemblages found in the upper intertidal or most sheltered sites, experience the least change per unit time, and may be considered more 'stable' (Lewis, 1977), if disturbed, these assemblages would recover much slower than lower intertidal and more exposed sites.

Habitat structure and complexity

The biotope consists of bedrock supporting large patches or a band of large, dense *Mytilus edulis*, which themselves support fucoids and a few red algae (Connor *et al.*, 1997b). The large patches of *Mytilus edulis* and barnacle covered substratum denote areas of different habitat complexity and species richness. Patches (or 'islands') of mussels support a diverse community (see Suchanek, 1985; Tsuchiya & Nishihira, 1985, 1986) whereas the interstices of barnacles provide shelter for small species (Barnes, 2000). The habitat complexity and species diversity of the shore depending on the relative abundance of mussel and barnacles, the presence of macroalgae and crevices.

Rock surface between mussel patches

- The rock surface may provide a complex of upward facing, overlapping and fissured habitats.
- The upward facing surfaces are likely to be colonized by limpets, barnacles and fucoids. Barnacles form a tightly packed covering over the substratum excluding other species. Dead barnacles leave gaps in the covering that can be exploited by small invertebrates. Small interstitial species occupy relatively stable microclimates in-between barnacles or in dead barnacles shells, including the small littorinids *Littorina neglecta* and *Littorina saxatilis*, the bivalve *Lasaea adansoni*, intertidal mites, amphipods and isopods (see Barnes, 2000 for review).
- Red foliose algae and encrusting coralline algae may be present, especially in the shelter of fucoids.
- Overhanging surfaces and fissures provide local shelter and may be colonized by sponges, hydroids and barnacles.
- The periphery of the mussel patches and beds attract feeding dog whelks *Nucella lapillus*.
- Wave sheltered large crevices and gullies provide refuges for dog whelks and littorinids, while crevices provide refuges for predatory nemertean and polychaetes (e.g. *Eulalia viridis*).

Patches or bands of mussels

Holt *et al.* (1998) noted that a raised bed was not present in this biotope and most associated organisms were capable of growing on the substratum in the absence of *Mytilus edulis*. The mussel bed can be divided into three distinct habitat components: the interstices within the mussel matrix; the biodeposits beneath the bed; and the substratum afforded by the mussel shells themselves (Suchanek, 1985; Seed & Suchanek, 1992). Although, the beds in this biotope are probably mostly composed of only a single layer of mussels, Tsuchiya & Nishihira (1985, 1986) demonstrated that old large mussels in Japan and mussel patches accumulated biogenic sediments and shell fragments. Please note that recent evidence suggests that the *Mytilus edulis* communities studied by Suchanek 1985 and Tsuchiya & Nishihira (1985 & 1986) were probably *Mytilus trossulus* and *Mytilus galloprovincialis* respectively (Seed, 1992), although their community structure is probably similar.

- The interstices between the mussels provide refuge from predation, and provide a humid environment protected from wave action, desiccation, and extremes of temperature. In the intertidal, *Mytilus* sp. beds the species richness and diversity increases with the age and size of the bed (Suchanek, 1985; Tsuchiya & Nishihira, 1985, 1986; Seed & Suchanek, 1992). The mussel matrix may support sea cucumbers, anemones, boring clionid sponges, ascidians, crabs, nemertean, errant polychaetes and flatworms (Suchanek, 1985;

Tsuchiya & Nishihira, 1985,1986).

- Mussel faeces and pseudo-faeces, together with silt, build up organic biodeposits under the beds, which support infauna such as sediment dwelling sipunculids, polychaetes and ophiuroids (Suchanek, 1978; Seed & Suchanek, 1992, Tsuchiya & Nishihira, 1985,1986). Flushing by wave action may prevent the build up of the thick layer of biodeposits found in *Mytilus* reefs.
- *Mytilus edulis* can use its prehensile foot to clean fouling organisms from its shell (Theisen, 1972). Therefore, the epizoan flora and fauna is probably less developed or diverse than found in beds of other mussel species but may include barnacles (e.g. *Elminius modestus*) and tubeworms (e.g. *Spirobranchus* species)
- Mobile epifauna include isopods, chitons (e.g. *Lepidochitona cinerea*) and gastropods such as littorinids (e.g. *Littorina littorea*) and top shells (e.g. *Steromphala umbilicalis*), which obtain refuge from predators, especially birds, within the mussel matrix, emerging at high tide to forage (Suchanek, 1985; Seed & Suchanek, 1992).
- Intense growth may occasionally give rise to hummocks in which the bed is raised off the surface and the available space colonized by small crabs and dog whelks (Seed & Suchanek, 1992; Davenport *et al.*, 1998).
- The mussels provide a substratum for the attachment of macroalgae such as *Fucus vesiculosus* and to a lesser extent other fucoids, foliose and filamentous algae e.g. *Ceramium* species, *Mastocarpus stellatus* and *Palmaria palmata*.

Fucoids and other macroalgae

- Where macroalgae are present the community also supports small crustaceans such as gammarid amphipods (e.g. *Hyale prevosti*) and isopods (e.g. *Idotea granulosa*) and gastropods (e.g. *Littorina obtusata* and *Littorina saxatilis*) (Tsuchiya & Nishihira, 1985,1986; Seed & Suchanek, 1992; JNCC, 1999). Ephemeral algae such as *Ulva* spp. and *Ulva lactuca* may also grow on the mussels themselves.

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.

Macroalgae such as *Fucus vesiculosus* are primary producers of organic carbon, which is utilized directly by grazing invertebrates. Raffaelli & Hawkins (1999) reported an estimate of the productivity of intertidal fucoids as 160 gC/m²/year in moderately wave exposed habitats. Only about 10% of the primary production is directly cropped by herbivores (Raffaelli & Hawkins, 1999). Macroalgae exude considerable amounts of 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 and may enter the food chain of local, subtidal ecosystems, or be exported further offshore.

Mytilus spp. communities are highly productive secondary producers (Seed & Suchanek, 1992; Holt *et al.*, 1998). Low shore mussels were reported to grow 3.5-4cm in 30 weeks and up to 6-8cm in length in 2 years under favourable conditions, although high shore mussels may only reach 2-3cm in length after 15-20 years (Seed, 1976). Seed & Suchanek (1992) suggested that in populations of older mussels, productivity may be in the region of 2000-14,500 kJ/m²/yr. In Killary Harbour,

western Ireland, the shore population of mussels contributed significantly to the larval population of the inlet. Kautsky (1981) reported that the release of mussel eggs and larvae from subtidal beds in the Baltic Sea contributed an annual input of 600 tons of organic carbon/yr. to the pelagic system. The eggs and larvae were probably an important food source for herring larvae and other zooplankton. Dense beds of bivalve suspension feeders increase turnover of nutrients and organic carbon in estuarine (and presumably coastal) environments by effectively transferring pelagic phytoplanktonic primary production to secondary production (pelagic-benthic coupling) (Dame, 1996). The *Mytilus edulis* beds probably also provide secondary productivity in the form of tissue, faeces and pseudofaeces (Seed & Suchanek, 1992; Holt *et al.*, 1998)

Recruitment processes

- *Mytilus edulis* recruitment is dependant on larval supply and settlement, together with larval and post-settlement mortality. Jørgensen (1981) estimated that larvae suffered a daily mortality of 13% in the Isefjord, Denmark but Lutz & Kennish (1992) suggested that larval mortality was approximately 99%. Larval mortality is probably due to adverse environmental conditions, especially temperature, inadequate food supply (fluctuations in phytoplankton populations), inhalation by suspension feeding adult mytilids, difficulty in finding suitable substrata and predation (Lutz & Kennish, 1992). Widdows (1991) suggested that any environmental factor that increased development time, or the time between fertilization and settlement would increase larval mortality.
- Recruitment in many *Mytilus* sp. populations is sporadic, with unpredictable pulses of recruitment (Seed & Suchanek, 1992). *Mytilus* sp. is highly gregarious and final settlement often occurs around or in-between individual mussels of established populations. Persistent mussel beds can be maintained by relatively low levels of recruitment e.g. McGrorty *et al.*, (1990) reported that adult populations were largely unaffected by large variations in spat fall between 1976-1983 in the Exe estuary.
- The *Mytilus edulis* bed may act as a refuge for larvae or juveniles, however, the intense suspension feeding activity of the mussels is likely to consume large numbers of pelagic larvae. Commito (1987) suggested that species that reproduce with cocoons, brood their young or disperse as juveniles will be favoured (see gastropods below).
- While *Asterias rubens*, for example, is widespread, and fecund, with a pelagic larvae capable of widespread dispersal, recruitment in starfish is sporadic, unpredictable and poorly understood (Seed, 1993).
- Barnacles such as *Semibalanus balanoides* have a planktonic nauplii larvae, which spends ca 2 months in the plankton, with high dispersal potential. Peak settlement in *Semibalanus balanoides* occurs in April-May in the west and May-June in the east and north of the British Isles, However, settlement intensity is variable, subsequent recruitment is inhibited by the sweeping action of macroalgal canopies (e.g. fucoids) or the bulldozing of limpets and other gastropods (see MarLIN review for details).
- The propagules of most macroalgae tend to settle near the parent plant (Schiel & Foster, 1986; Norton, 1992; Holt *et al.*, 1997). For example, the propagules of fucales are large and sink readily and red algal spores and gametes are immotile. Norton (1992) noted that algal spore dispersal is probably determined by currents and turbulent deposition (zygotes or spores being thrown against the substratum). For example, spores of *Ulva* spp. have been reported to travel 35km, *Phycodrys rubens* 5km and *Sargassum muticum* up to 1km, although most *Sargassum muticum* spores settle within 2m. The reach of the furthest propagule and useful dispersal range are not the same thing and recruitment usually occurs on a local scale, typically within 10m of the parent plant (Norton, 1992). Vadas *et al.* (1992) noted that post-settlement mortality of algal propagules and early germlings was

high, primarily due to grazing, canopy and turf effects, water movement and desiccation (in the intertidal) and concluded that algal recruitment was highly variable and sporadic. However, macroalgae are highly fecund and widespread in the coastal zone so that recruitment may be still be rapid, especially in the rapid growing ephemeral species such as *Ulva* spp. and *Ulva lactuca*, which reproduce throughout the year with a peak in summer. Similarly, *Ceramium* species produce reproductive propagules throughout the year, while *Mastocarpus stellatus* produce propagules from February to December, and exhibit distinct reproductive papillae in summer (Dixon & Irvine, 1977; Burrows, 1991; Maggs & Hommersand, 1993).

- Gastropods exhibit a variety of reproductive life cycles. The common limpet *Patella vulgata*, the top shell *Steromphala umbilicalis*, and *Littorina littorea* have pelagic larvae with a high dispersal potential, although recruitment and settlement is probably variable. However, *Littorina obtusata* lays its eggs on the fronds of fucoids from which hatch crawl-away miniature adults. Similarly, the dog whelk *Nucella lapillus* lays egg capsules on hard substrata in damp places on the shore, from which crawl-aways emerge. Therefore, their dispersal potential is limited but probably designed to colonize an abundant food source. In addition, most gastropods are relatively mobile, so that a large proportion of recruitment of available niches within a mussel bed would involve migration. *Nucella lapillus* is an exception, as they generally do not move far, averaging 100mm /tidal cycle, or between 30cm or 10m per year when in the vicinity of an abundant food source (see MarLIN reviews for details; Fish & Fish, 1996).
- Many species of mobile epifauna, such as polychaetes that may be associated with patches of mussels or rock crevices, have long lived pelagic larvae and/or are highly motile as adults. Gammarid amphipods brood their embryos and offspring but are highly mobile as adults and probably capable of colonizing new habitats from the surrounding area (e.g. see *Hyale prevosti* review).

Time for community to reach maturity

Development of the community from bare or denuded rock is likely to follow a similar succession to that occurring after an oil spill. The loss of grazing species results in an initial proliferation of ephemeral green then furoid algae, which then attracts mobile grazers, and encourages settlement of other grazers. Limpet grazing reduces the abundance of fucoids allowing barnacles to colonize the shore. Recovery of rocky shore populations was intensively studied after the *Torrey Canyon* oil spill in March 1967. Areas affected by oil alone recovered rapidly, within 3 years. But other sites suffered substantial damage due to the spilled oil and the application of aromatic hydrocarbon based dispersants. In the latter sites, populations of fucoids were abnormal for the first 11 years, and limpet *Patella vulgata* populations were abnormal for at least 10-13 years. Recovery rates were dependant on local variation in recruitment and mortality so that sites varied in recovery rates, for example maximum cover of fucoids occurred within 1-3 years, barnacle abundance increased in 1-7 years, limpet number were still reduced after 6-8 years and species richness was regained in 2 to >10 years. Overall, recovery took 5-8 years on many shores but was estimated to take about 15 years on the worst affected shores (Southward & Southward, 1978; Hawkins & Southward, 1992; Raffaelli & Hawkins, 1999).

This biotope is characterized by the presence of dense *Mytilus edulis*. *Mytilus* spp. populations were considered to have a strong ability to recover from environmental disturbance (Holt *et al.*, 1998; Seed & Suchanek, 1992). Larval supply and settlement could potentially occur annually, however,

settlement is sporadic with unpredictable pulses of recruitment (Lutz & Kennish, 1992; Seed & Suchanek, 1992). The presence of macroalgae in disturbance gaps in *Mytilus californianus* populations, where grazers were excluded, inhibited recovery by the mussels. In New England, U.S.A, prior barnacle cover was found to enhance recovery by *Mytilus edulis* (Seed & Suchanek, 1992). While good annual recruitment is possible, recovery of the mussel population may take up to 5 years. However, recovery of the mussel population may be delayed by 1-7 years for the initial macroalgal cover to reduce and barnacle cover to increase. Therefore, the biotope may take between 5 -10 years to recover depending on local conditions.

Once, the patches of mussels have returned colonization of the associated community is dependant on the development of a mussel matrix, younger beds exhibiting lower species richness and species diversity than older beds, and hence growth rates and local environmental conditions. Tsuchiya & Nishihira (1986) examined young and older patches of *Mytilus* (probably *Mytilus galloprovincialis*) in Japan. They noted that as the patches of mussels grew older, individuals increased in size, and other layers were added, increasing the space within the matrix for colonization, which also accumulated biogenic sediment. Increased space and organic sediment was then colonized by infauna and epiphytes and as the patches and mussels became older, eventually epizotic species colonized the mussel shells. Macroalgae could colonize at any time in the succession. Tsuchiya & Nishihira (1986) did not suggest a timescale.

Additional information

None entered

Preferences & Distribution

Habitat preferences

Depth Range	Mid shore
Water clarity preferences	
Limiting Nutrients	Data deficient
Salinity preferences	Full (30-40 psu)
Physiographic preferences	Enclosed coast / Embayment, Open coast, Strait / sound
Biological zone preferences	Eulittoral
Substratum/habitat preferences	Bedrock, Large to very large boulders
Tidal strength preferences	
Wave exposure preferences	Exposed, Moderately exposed
Other preferences	Gentle slopes or horizontal platforms

Additional Information

This biotope has been identified at locations with very different environmental conditions. It appears to occur in waters that are highly turbid (e.g. the east basin of the Irish Sea and north east England) and in waters with low turbidity (e.g. Shetland). It may be a predominantly turbid water biotope where mussels thrive as a result of high suspended sediment levels and fucoids survive due to moderate wave shelter.

The upper limit of the mussel bed is often clear cut (see Lewis, 1964) and determined by physical factors such as temperature and desiccation, which may be synergistic, i.e. sudden mass mortalities at the upper limit of intertidal mussel beds are often associated with prolonged periods of unusually high temperatures and desiccation stress (Seed & Suchanek, 1992).

The lower limit of distribution is strongly influenced by predation, primarily from starfish but also dogwhelks and crabs. For example, on the east coast of England, the starfish *Asterias rubens* and the dogwhelk *Nucella lapillus* eliminate mussels from the lower intertidal (Seed, 1969). In Ireland, however, the lower limit is probably controlled by the crabs *Carcinus* sp. and *Liocarcinus* sp., the dogwhelk *Nucella lapillus* and the starfish *Marthasterias glacialis* (Kitching & Ebling, 1967; Seed & Suchanek, 1992; Holt *et al.*, 1998).

Mussels colonize areas denuded of barnacles by sediment scour, and are tolerant of a degree of sediment scour (Lewis, 1964). However, increased scour may also limit the lower extent of the mussel bed (Holt *et al.*, 1998).

Connor *et al.* (1997) noted that sediment often occurs in the vicinity of this biotope, and the biotope may be silted. Tsuchiya & Nishihira (1985 & 1986) noted that increase sediment or silt build up within the mussel bed matrix, reduced the available space within the matrix, changing species composition, presumably in favour of infaunal invertebrates, and reduced species richness.

Species composition

Species found especially in this biotope

- *Ceramium shuttleworthianum*

Rare or scarce species associated with this biotope

-

Additional information

Long-lived, stable mussel beds on moderately exposed rocky shores (e.g. this biotope) develop diverse species communities with typically 50-100 species (Seed, 1996; Holt *et al.*, 1998). Tsuchiya & Nishihira (1985 & 1986) give detailed species lists for intertidal *Mytilus edulis* patches in Japan, which demonstrate the potential species richness of similar habitats. The MNCR reported 128 species from this biotope, although not all species occur in all examples of the biotope (JNCC, 1999).

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

The biotope description and information on characteristic features is taken from Connor *et al.* (2004). The sensitivity assessments specifically consider the named species characterizing this biotope; the blue mussel *Mytilus edulis* which occurs as a dense band or large patches and the brown seaweed *Fucus vesiculosus*. These species define the biotope and provide complex habitats that shelter species and modify environmental conditions. The loss of these species, in particular *Mytilus edulis*, would lead to reclassification of the biotope.

A number of other species typically found on rocky shores are usually present in this biotope including occasional red seaweeds such as *Porphyra umbilicalis*, *Osmundea pinnatifida*, *Mastocarpus stellatus*, *Palmaria palmata* or the calcareous algae *Corallina officinalis*. The ephemeral green seaweeds *Ulva intestinalis* and *Ulva lactuca* commonly occur on the shells of the mussels. The barnacle *Semibalanus balanoides* and mobile species including *Patella vulgata*, the winkle *Littorina littorea* and the whelk *Nucella lapillus* also occur. The associated species increase species diversity and support the delivery of ecosystem function and goods and services in general. Predation by *Nucella lapillus* and grazing by *Littorina littorea* and *Patella vulgata* may structure the mussel assemblage and the algae, respectively. Barnacles, *Semibalanus balanoides* interact with the other associated species and hence may structure the assemblage. The sensitivity of these species is considered generally and where pressures may lead to changes in abundance that would alter the biotope character.

The biotope is dependent on the environmental habitat factors including the presence of hard substratum. The effects of wave exposure and sand abrasion may also be important factors preventing domination by fucoids in this biotope. These factors are therefore considered within the sensitivity assessments where they may be altered by the pressure.

Resilience and recovery rates of habitat

The algae within the biotope can regrow damaged fronds and blades and may regrow from perennial holdfasts or crustose bases, where these remain. *Mytilus edulis* and other molluscs may be able to repair shells following minor damage but will be more vulnerable to predators and desiccation while recovering. Unlike the animal species macroalgae have short dispersal distances, over tens of metres (Dudgeon *et al.*, 2001) and therefore recovery will require the presence of adults.

Where populations of animals and macroalgae are entirely removed (resistance is 'None') recovery will require recolonization by propagules. Adults of the mobile species present in the biotope, such as limpets and littorinids may recolonize through adult migration into the habitat from adjacent populations following disturbance or via larval recolonization. In general the animals within the biotope produce high numbers of pelagic larvae which are widely distributed by water currents, supporting recolonization from surrounding populations following disturbances. Conversely the characterizing and associated macroalgae generally produce eggs which sink rapidly to the substratum in the vicinity of the adult plants. Recovery of algal populations may be rapid where adults remain but prolonged where populations are entirely removed.

Mainwaring *et al.* (2014) reviewed the evidence for recovery of *Mytilus edulis* beds from disturbance and an earlier study by Seed & Suchanek (1992) reviewed studies on the recovery of

'gaps' in *Mytilus* spp. beds. It was concluded that beds occurring high on the shore and on less exposed sites took longer to recover after a disturbance event than beds found low on the shore or at more exposed sites. However, the slowest recovering sites (high shore and sheltered shores) are at the least risk of natural disturbance and often considered more 'stable' (Lewis, 1964) as they are less vulnerable to removal by wave action or wave driven logs. Continued disturbance will lead to a patchy distribution of mussels.

Recruitment of *Mytilus edulis* is often sporadic, occurring in unpredictable pulses (Seed & Suchanek, 1992), although persistent mussel beds can be maintained by relatively low levels or episodic recruitment (McGrorty *et al.*, 1990). A good annual recruitment could result in rapid recovery (Holt *et al.*, 1998). However, the unpredictable pattern of recruitment based on environmental conditions could result in recruitment taking much longer. In the northern Wadden Sea, strong year classes (resulting from a good recruitment episode) that lead to rejuvenation of blue mussel beds are rare, and usually follow severe winters, even though mussel spawning and settlement are extended and occur throughout the year (Diederich, 2005). In the List tidal basin (northern Wadden Sea) a mass recruitment of mussels occurred in 1996 but had not been repeated by 2003 (the date of the study), i.e. for seven years (Diederich, 2005).

In long-term studies of *Mytilus californianus*, it was observed that gaps continued to increase in size post disturbance due to wave action and predation (Paine & Levin, 1981; Brosnan & Crumrine, 1994; Smith & Murray, 2005) potentially due to the weakening of the byssus threads leaving them more vulnerable to environmental conditions (Denny 1987). On rocky shores barnacles and fucoids are often quick to colonize the 'gaps' created. The presence of macroalgae appears to inhibit recovery whilst the presence of barnacles enhances subsequent mussel recruitment (Seed & Suchanek, 1992). Brosnan & Crumrine (1994) observed little recovery of the congener *Mytilus californianus* in two years after trampling disturbance. Paine & Levin (1981) estimated that recovery times of beds could be between 8-24 years while Seed & Suchanek (1992) suggested it could take longer-time scales, suggesting that meaningful recovery is unlikely in some areas. It has, however, been suggested that *Mytilus edulis* recovers quicker than other *Mytilus* species (Seed & Suchanek, 1992), which may mean that these predicted recovery rates are too low for *Mytilus edulis*.

Mytilus edulis is highly fecund, producing >1,000,000 eggs per spawning event. Larvae stay in the plankton for between 20 days to two months depending on water temperature (Bayne, 1976). In unfavourable conditions they may delay metamorphosis for 6 months (Lane *et al.*, 1985). Larval dispersal depends on the currents and the length of time they spend in the plankton. Settlement occurs in two phases, an initial attachment using their foot (the pediveliger stage) and then a second attachment by the byssus thread before which they may alter their location to a more favourable one (Bayne, 1964). The final settlement often occurs around or between individual mussels of an established population. In areas of high water flow the mussel bed will rely on recruitment from other populations as larvae will be swept away and therefore recovery will depend on recruitment from elsewhere.

Larval mortality can be as high as 99% due to adverse environmental conditions, especially temperature, inadequate food supply (fluctuations in phytoplankton populations), inhalation by suspension feeding adult mytilids, difficulty in finding suitable substrata and predation (Lutz & Kennish 1992). After settlement the larvae and juveniles are subject to high levels of predation as well as dislodgement from waves and sand abrasion depending on settlement site. Height on the shore generally determines lifespan with mussels in the low shore only surviving between 2-3 years due to high predation levels whereas higher up on the shore a wider variety of age classes

are found (Seed, 1969). Theisen (1973) reported that specimens of *Mytilus edulis* could reach 18-24 years of age.

The key characterizing species *Fucus vesiculosus* recruits readily to cleared areas of the shore and full recovery has been demonstrated to occur in 1-3 years in British waters (Hartnoll & Hawkins, 1985). Keser & Larson (1984) investigated the recovery of *Fucus vesiculosus* to plots which had been scraped clean and burned with a propane torch. *Fucus vesiculosus* was the first perennial alga to colonize the experimentally denuded transects, even at sites and tidal levels that had been dominated by *Ascophyllum* or *Chondrus crispus* beforehand. Recovery occurred at all sites between 3 to 21 months. The study found newly settled germlings of *Fucus vesiculosus* in most months, indicating an extended reproductive period (Keser & Larson, 1984).

When grazers are excluded from areas of intertidal shores fucoids have the ability to rapidly recolonize areas, they can even be found in zones on rocky shores where they do not normally occur (Burrows & Lodge, 1950, Southward & Southward, 1978). Fucoid distributions return to their recognized zones when grazers are re-established on a shore (Burrows & Lodge, 1950, Southward & Southward, 1978). Although intertidal shores can rapidly regain fucoids it can take considerably longer for typical ecosystem function to return if grazers have also been lost (Hawkins & Southward, 1992). If the whole community is removed, recovery is likely to occur at a much lower pace. Indeed, Hawkins & Southward (1992) found that, after the M.V. *Torrey Canyon* oil spill, it took between 10 and 15 years for the *Fucus* spp. to return to 'normal' levels of spatial and variation in cover on moderately exposed shores. Therefore, for factors which are likely to totally remove the population over a wide area, recoverability is likely to be prolonged.

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

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

limiting factor in reproduction in this species (Serrão *et al.*, 2000).

Fucus vesiculosus mortality is extremely high in the early stages of germination up to a time when plants are 3 cm in length and this is due mostly to grazing (Knight & Parke 1950). While *Fucus vesiculosus* may resist some degree of environmental stress, their long-term persistence depends on their reproductive ability as well as the survival and growth of early life history stages (germlings) that are generally more susceptible to natural and anthropogenic stressors than adults (Steen, 2004; Fredersdorf *et al.*, 2009). It is therefore necessary to include early life stage responses in the assessment of effects of environmental changes on fucoid algae as only considering fully developed adults specimens may lead to false conclusions (Nielsen *et al.*, 2014).

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

Red algae may recruit rapidly or regrow from crustose bases and holdfasts, although rates and pathways may vary seasonally. *Corallina officinalis* was shown to settle on artificial substances within 1 week of their placement in the intertidal in New England summer (Harlin & Lindbergh, 1977). However, settlement plates laid out in the autumn were not recolonized until the next spring. In the lower rocky intertidal in southern California dominated by *Corallina officinalis* with foliose overstorey algae present, Littler & Kauker (1984) experimentally cleared plots and followed the recovery for 12 months. Some areas were scraped allowing the basal crusts to remain whereas others were completely sterilised (removal of all material and surfaces then scorched with a blow torch to remove bases). In scraped plots up to 15% cover of *Corallina officinalis* fronds returned within 3 months after removal of fronds and all other epiflora/fauna (Littler & Kauker, 1984) while in sterilized plots (all basal crusts removed) appearance of articulated fronds occurred 6 months following clearance. At the end of the 12 month observation period *Corallina officinalis* cover had increased to approximately 18% in plots where basal crusts remained and to approximately 10% in sterilised plots. Similarly Bamber & Irving (1993) reported that new plants grew back in scraped transects within 12 months, although the resistant crustose bases were probably not removed.

The green algae associated with this biotope are classified as opportunistic species that are able to rapidly colonize newly created gaps across a range of sediment types, shore heights, wave exposures and salinity regimes. *Ulva* sp. release zoospores and gametes (collectively called swimmers) to the water column in high numbers during extended reproduction periods (Smith, 1947). Swimmers are capable of dispersal over a considerable distance, for instance, Amsler & Searles (1980) showed that swimmers of a coastal population of *Ulva* (as *Enteromorpha*) reached exposed artificial substrata on a submarine plateau 35 km away. *Ulva intestinalis* is amongst the first multicellular algae to appear on substrata that have been cleared following a disturbance, e.g. following the *Torrey Canyon* oil spill in March 1967, species of the genus *Ulva* rapidly recruited to areas where oil had killed the herbivores that usually grazed on them, so that a rapid greening of the rocks (owing to a thick coating of *Ulva* spp.) was apparent by mid-May (Smith, 1968).

Other species that are associated with this biotope, including the limpet *Patella vulgata*, the barnacle *Semibalanus balanoides* and littorinids generally have slower recovery rates due to episodic recruitment and slower growth. Where individuals are removed from a small area, adult limpets and *Littorina saxatilis* may recolonize from surrounding patches of habitat where these are present. The barnacles and limpets and the winkle *Littorina littorea* are common, widespread species that spawn annually producing pelagic larvae that can disperse over long distances. It is therefore likely that adjacent populations will provide high numbers of larvae, although recruitment may be low due to habitat unsuitability and the presence of dense *Ulva* spp. preventing settlement on rock surfaces. *Littorina saxatilis* however brood young and do not have a pelagic life stage, recovery will therefore depend on the presence of adults in close proximity to impacted areas.

Resilience assessment. The evidence for recovery rates of *Mytilus edulis* beds from different levels of impact is very limited and whether these rates are similar, or not, between different type of biotope is largely unclear. Recovery rates are clearly determined by a range of factors such as degree of impact, season of impact, larval supply and local environmental factors including hydrodynamics so that confidence in the applicability of generic assessments is 'Low'. Overall, *Mytilus* spp. populations are considered to have a strong ability to recover from environmental disturbance (Holt *et al.*, 1998; Seed & Suchanek, 1992). A good annual recruitment may allow a bed to recovery rapidly, though this cannot always be guaranteed within a certain time-scale due to the episodic nature of *Mytilus edulis* recruitment (Lutz & Kennish, 1992; Seed & Suchanek, 1992) and the influence of site-specific variables. Resilience will vary depending of larval supply and wave exposure with areas with low larval supply and high wave exposure on sandy substrata experiencing the longest recovery rates. The sensitivity assessments for this biotope have adopted the rates of *Mytilus edulis* recovery used by Mainwaring *et al.* (2014) as this species and the dense bands it forms may be the slowest element to recover. Where biotope resistance is 'High' then there is no effect to recover from and resilience should be assessed as 'High'. Littoral and sublittoral beds or dense patches of *Mytilus edulis* are considered to have 'Medium' resilience (2 - 10 years) to represent the potential for recovery within a few years where a proportion of the bed remains ('Medium' or 'Low' resistance). Resilience of *Mytilus edulis* is assessed as 'Low' (over 10 years) for all biotopes where resistance is assessed as 'None', as recovery is dependent on recruitment from other areas and recruitment can be sporadic. Due to the variation in recovery rates reported in the literature, while the evidence for resilience is of 'High' quality and 'High' applicability (for recovery from the same pressures or otherwise assessed as 'Low'), the degree of concordance is 'Medium'.

The characterizing species *Fucus vesiculosus* and the turf forming red algae are considered to have higher recovery rates than *Mytilus edulis*. Where holdfasts/crustose bases remain recovery will occur by regrowth. *Corallina officinalis* has crustose bases that are more resistant to desiccation, heat and scour than the fronds, the bases may grow occupying more space, while other red algae have long-lived holdfasts. The algae may therefore recover before the *Mytilus edulis* patches. If specimens of *Fucus vesiculosus* remain in small quantities it is likely that re-growth will occur rapidly due to efficient fertilization rates and recruitment over short distances. Recovery is likely to occur within two years resulting in a 'High' resilience score. However, if the population is removed (resistance is 'None'), recovery may take longer, perhaps up to 10 years (as seen after the *M.V. Torrey Canyon* oil spill) so the resilience would be scored as 'Medium'.

It is likely that habitats where this biotope grows may undergo much temporal variation mediated by disturbance (particularly sediment scour), competition for space and grazing. The grazers are a key component of this biotope and will influence the dynamics of the biotope. Changes and

recovery trajectories following the removal of key species are unpredictable and interactions between the key species may be positive or negative. Limpets and littorinids may enhance barnacle settlement by grazing and removing algae (Hawkins, 1983) or by depositing pedal mucus trails that attract barnacle larvae (Holmes *et al.*, 2005). Barnacles and small clumps of *Mytilus edulis* may enhance survival of small limpets by moderating environmental stresses but they may also have negative effects on recruitment by occupying space and by limiting access to grazing areas (Lewis & Bowman (1975). Mrowicki *et al.*, (2014) found that limpet and barnacle removal allowed ephemeral and furoid macroalgae to establish on sheltered and wave exposed shores in Ireland. Dense coverings of mussels and fucoids, however, inhibit settlement of larvae through competition for space or prevention of settlement (Lewis & Bowman, 1975). On the wave exposed and scoured shores that this biotope occurs on, grazing may limit initial settlement of macroalgae but wave action will limit the presence of adults and larger species through, breakage and drag effects leading to loss.

NB: 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 recognizable as the initial habitat of interest. It should be noted that the recovery rates are only indicative of the recovery potential.

Hydrological Pressures

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

Species found in the intertidal are exposed to extremes of high and low air temperatures during periods of emersion. They must also be able to cope with sharp temperature fluctuations over a short period of time during the tidal cycle. In winter, air temperatures are colder than the sea, conversely in summer air temperatures are much warmer than the sea. Species that occur in this intertidal biotope are therefore generally adapted to tolerate a range of temperatures, although the timing of site-specific factors such as low tides will influence local acclimation. For intertidal species increased temperatures may also result in desiccation when exposed (see changes in emergence pressure). Local populations may be acclimated to the prevailing temperature regime and may therefore exhibit different tolerances to other populations subject to different conditions and therefore caution should be used when inferring tolerances from populations in different regions.

Mytilus edulis is a eurytopic species found in a wide temperature range from mild, subtropical regions to areas which frequently experience freezing conditions and are vulnerable to ice scour (Seed & Suchanek, 1992). In recent years, *Mytilus edulis* has been observed to be expanding its range pole-wards and has reappeared in Svalbard, due to an increase of sea temperature in that region (Berge *et al.*, 2005), whilst its equatorial limits are contracting due to increases in water temperature beyond the lethal limit (Jones *et al.*, 2010). In British waters 29°C was recorded as

the upper sustained thermal tolerance limit for *Mytilus edulis* (Read & Cumming, 1967; Almada-Villela, *et al.*, 1982), although it is thought that European mussels will rarely experience temperatures above 25°C (Seed & Suchanek, 1992).

Tsuchiya (1983) documented the mass mortality of *Mytilus edulis* in Mutsu Bay, northern Japan in August 1981 due to air temperatures of 34°C that resulted in mussel tissue temperatures in excess of 40°C. In one hour, 50% of the *Mytilus edulis* from the upper 75% of the shore had died. It could not be concluded from this study whether the mortality was due to high temperatures, desiccation or a combination of the two. Lethal water temperatures appear to vary between areas (Tsuchiya, 1983) although it appears that their tolerance at certain temperatures vary, depending on the temperature range to which the individuals are acclimatised (Kittner & Riisgaard, 2005). After acclimation of individuals of *Mytilus edulis* to 18°C, Kittner & Riisgaard (2005) observed that the filtration rates were at their maximum between 8.3 and 20°C and below this at 6°C the mussels closed their valves. However, after being acclimated at 11°C for five days, the mussels maintained the high filtration rates down to 4°C. Hence, given time, mussels can acclimatise and shifting their temperature tolerance. Filtration in *Mytilus edulis* was observed to continue down to -1°C, with high absorption efficiencies (53-81%) (Loo, 1992).

At the upper range of a mussels tolerance limit, heat shock proteins are produced, indicating high stress levels (Jones *et al.*, 2010). After a single day at 30°C, the heat shock proteins were still present over 14 days later, although at a reduced level. Increased temperatures can affect reproduction in *Mytilus edulis* (Myrand *et al.*, 2000). In shallow lagoons mortality began in late July at the end of a major spawning event when temperatures peaked at >20°C. These mussels had a low energetic content post spawning and had stopped shell growth. It is likely that the high temperatures caused mortality due to the reduced condition of the mussels post spawning (Myrand *et al.*, 2000). Gamete production does not appear to be affected by temperature (Suchanek, 1985).

Temperature changes may also lead to indirect effects. For example, an increase in temperature increases the mussels' susceptibility to pathogens (*Vibrio tubiashii*) in the presence of relatively low concentrations of copper (Parry & Pipe, 2004). Increased temperatures may also allow for range expansion of parasites or pathogens which will have a negative impact upon the health of the mussels if they become infected. Power stations have the potential to cause an increase in sea temperature of up to 15°C (Cole *et al.*, 1999), although this impact will be localised. However, as mussels are of the most damaging biofouling organisms on water outlets of power stations, they are clearly not adversely affected (Whitehouse *et al.*, 1985; Thompson *et al.*, 2000).

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

Littler & Kauker (1984) suggested that the crustose bases of *Corallina officinalis* are more resistant of desiccation or heating than fronds. Lüning (1990) reported that *Corallina officinalis* from Helgoland survived one week exposure to temperatures between 0°C and 28°C. Latham (2008) investigated the effects of temperature stress on *Corallina officinalis* through laboratory tests on samples collected in the Autumn in Devon, (England) from rockpools. Samples were kept at 15 °C for three days and then exposed to temperatures of 5 °C, 15 °C, 20 °C, 25 °C and 30 °C (the normal

range of temperature experienced was suggested to be between 5 and 15 °C). At 35 °C the *Corallina* was completely bleached after 3 days with a sample kept at 30 °C beginning to bleach. After 7 days (the end of the experiment) the sample kept at 30 °C was partially bleached. Samples kept at 5, 15, 20 and 25 °C showed little change in chemicals produced in reaction to thermal stress and no bleaching suggesting the temperatures in that range had not induced stress reactions.

In an exceptionally hot summer (1983, with an increase of between 4.8 and 8.5 °C), Hawkins & Hartnoll (1985) observed no temperature bleaching of adult *Himanthalia elongata* (although some buttons were bleached) or other canopy forming species. However, understorey red algae showed more signs of damage with bleached *Corallina officinalis* observed around the edges of pools due to desiccation. Occasional damaged specimens of *Palmaria palmata*, *Osmundea pinnatifida* and *Mastocarpus stellatus* were observed. *Palmaria palmata* does well in low temperatures, with an optimum between 6 and 15°C, consistent with a distribution in northern temperate and arctic waters. This species is also found in warmer temperate waters as far south as Portugal in Europe and with localized large populations in northern Spain (Garbary *et al.*, 2012 and references therein). Temperatures at or above 15°C may induce physiological stress (Werner & Fring, 2011; Morgan *et al.*, 1980). In tank cultures of *Palmaria palmata* at 20°C and above, all plants were dead within a week (Morgan *et al.*, 1980). Populations may be acclimated to typical conditions but it is likely that *Palmaria palmata* may be bleached or damaged by higher than usual temperatures.

Ulva spp. are characteristic of upper shore rock pools, where water and air temperatures are greatly elevated on hot days. Empirical evidence for thermal tolerance to anthropogenic increases in temperature is provided by the effects of heated effluents on rocky shore communities in Maine, USA. *Ascophyllum* and *Fucus* were eliminated from a rocky shore heated to 27-30°C by a power station whilst *Ulva intestinalis* (as *Enteromorpha intestinalis*) increased significantly near the outfall (Vadas *et al.*, 1976).

Limpets, *Patella vulgata* and littorinids also occur within this biotope. Laboratory studies suggest that adults of these species can tolerate temperature increases. The median upper lethal temperature limit in laboratory tests on *Littorina littorea*, *Littorina saxatilis* was approximately 35 °C (Davenport & Davenport, 2005). *Patella vulgata* can also tolerate high temperatures. The body temperature of *Patella vulgata* can exceed 36°C in the field, (Davies, 1970); adults become non-responsive at 37-38°C and die at temperatures of 42°C (Evans, 1948). *Semibalanus balanoides* and *Patella vulgata* are 'northern' with their range extending from Portugal or Northern Spain to the Arctic circle. Populations in the southern part of England are therefore relatively close to the southern edge of their geographic range. Reproductive and recruitment success in both species is linked to temperature and long-term changes in temperature (exceeding the duration of the pressure benchmark) may lead to replacement by the warm water species *Chthamalus montagui* and *Chthamalus stellatus* (Southward *et al.*, 1995). In Northern Portugal warming seas appear to be linked to a shortening of the reproductive period and the lack of multiple spawning events in *Patella vulgata* and other northern species (Ribeiro *et al.*, 2009).

Sensitivity assessment. Based on the wide range of temperature tolerance of *Mytilus edulis* and its limited effect on its physiology, it is concluded that the acute and chronic changes described by the benchmarks of 2-5°C would have limited effect. *Fucus vesiculosus* are found in the middle of their natural temperature range in the British Isles and are therefore not likely to be affected by an increase in temperature at the pressure benchmark. The characterizing and associated species are considered to have 'High' resistance to changes in temperature at the pressure benchmark, although some of the understorey of red algae may be lost during acute temperature increases if

these occur in the summer when plants are already close to the limit of thermal tolerances. Biotope resistance is assessed as 'High' and resilience as 'High' and the biotope is considered to be 'Not sensitive'. It should be noted that the timing of acute and chronic increases would alter the degree of impact and hence sensitivity. An acute change occurring on the hottest days of the year and exceeding thermal tolerances may lead to mortality. Sensitivity of *Patella vulgata* and *Semibalanus balanoides* to longer-term, broad-scale perturbations would potentially be greater due to effects on reproduction.

Temperature decrease (local)

High

Q: High A: High C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: High

Many intertidal species are tolerant of freezing conditions as they are exposed to extremes of low air temperatures during periods of emersion. They must also be able to cope with sharp temperature fluctuations over a short period of time during the tidal cycle. In winter air temperatures are colder than the sea, conversely in summer air temperatures are much warmer than the sea. Species that occur in the intertidal are therefore generally adapted to tolerate a range of temperatures, with the width of the thermal niche positively correlated with the height of the shore (Davenport & Davenport, 2005). Local populations may be acclimated to the prevailing temperature regime and may therefore exhibit different tolerances to other populations subject to different salinity conditions and therefore caution should be used when inferring tolerances from populations in different regions. *Mytilus edulis* is a eurytopic species found in a wide temperature range from mild, subtropical regions to areas which frequently experience freezing conditions and are vulnerable to ice scour (Seed & Suchanek, 1992).

The lower lethal limit of *Mytilus edulis* depends on the length of time exposed to a low temperature and the frequency of exposure (Bourget, 1983). Williams (1970) observed that *Mytilus edulis* tolerated a tissue temperature as low as -10°C . In a laboratory experiment, Bourget (1983) showed that the median lethal temperature for 24 hour of exposure in *Mytilus edulis* was -16°C for large mussels (>3 cm) and -12.5°C for juveniles (<1.5 cm). However, when exposed to reduced temperatures for only 16 hours, the median lethal temperature of large mussels decreased to -20°C . It was also reported that mussels exposed to sub lethal temperatures cyclically, e.g. -8°C every 12.4 hours for 3-4 days, suffered significant damage likely to lead to death (Bourget, 1983), which suggested that while *Mytilus edulis* could tolerate occasional sharp frost events it was not likely to survive prolonged periods of very low temperatures. During the cold winter of 1962/63, *Mytilus edulis* was reported to have experienced relatively few effects with only 30% mortality being recorded from the south east coast of England (Whitstable area) and only about 2% mortality was reported from Rhosilli in South Wales (Crisp, 1964). Crisp (1964) also noted that the mortality was mainly from predation on the individuals that were weakened by the low temperatures rather than the temperature itself. It is thought that the use of nucleating agents in the haemolymph and the maintenance of a high osmotic concentration in the mantle fluid during periods of winter isolation allows *Mytilus edulis* to tolerate such low temperatures (Aunaas *et al.*, 1988).

Shell growth is not expected to be majorly influenced by low temperatures. Bayne (1976) demonstrated that between 10 - 20°C water temperature had little effect on scope for growth, similar to the findings of (Page & Hubbard, 1987) who found that a temperature range of 10 - 18°C did not influence growth rate. In addition, Loo (1992) recorded growth rates of up to 0.7% at temperatures as low as -1°C , with an excess of seston, a rate higher than the same author recorded in mussel culture in Sweden (Loo & Rosenberg, 1983). They concluded that food availability was

more of a limiting factor to growth than temperature (Loo, 1992).

In the north east Atlantic *Fucus vesiculosus* occurs from Northern Russia to Morocco (Powell, 1963). Within this range *Fucus vesiculosus* can survive in a wide variety of temperatures. *Fucus vesiculosus* also tolerates extended periods of freezing in the northern part of its range.

Under extremely low temperatures, components of the community demonstrate tolerance. Lüning (1990) reported that *Corallina officinalis* from Helgoland survived 0°C when exposed for one week. New Zealand specimens were found to tolerate -4°C (Frazer *et al.*, 1988). Lüning (1990) suggested that most littoral algal species were tolerant of cold and freezing. The associated species *Mastocarpus stellatus* has a broad geographical distribution (Guiry & Guiry, 2015) and throughout the range experience wide variation in temperatures (although local populations may be acclimated to the prevailing thermal regime). The photosynthetic rate of *Mastocarpus stellatus* higher on the shore fully recovered from 24 hrs at -20°C (Dudgeon *et al.* (1989). Photosynthesis in *Mastocarpus stellatus* also recovered quickly after experimental freezing (Dudgeon *et al.*, 1989, 1995). *Palmaria palmata* does well in low temperatures, with an optimum between 6 and 15°C, consistent with a distribution in northern temperate and arctic waters. In the laboratory, plants only became fertile if left at temperatures between 5-7°C with a short light period (Meer van der, 1979). Acute or chronic changes in temperature below 5 °C may therefore reduce reproductive success although reproduction and vegetative growth in warmer months should compensate for any reduction in output. The green algae, *Ulva* spp. are eurytopic, found in a wide temperature range and in areas which frequently experience freezing conditions and are vulnerable to ice scour (Seed & Suchanek 1992).

The tolerance of *Semibalanus balanoides* collected in the winter (and thus acclimated to lower temperatures) to low temperatures was tested in the laboratory. The median lower lethal temperature tolerance was -14.6 °C (Davenport & Davenport, 2005). A decrease in temperature at the pressure benchmark is therefore unlikely to negatively affect this species. The same series of experiments indicated that median lower lethal temperature tolerances for *Littorina saxatilis* and *Littorina littorea* were -16.4 and -13°C respectively. Adults of *Patella vulgata* are also largely unaffected by short periods of extreme cold. Ekaratne & Crisp (1984) found adult limpets continuing to grow over winter when temperatures fell to -6 °C, and stopped only by still more severe weather. However, loss of adhesion after exposure to -13°C has been observed with limpets falling off rocks and therefore becoming easy prey to crabs or birds (Fretter & Graham, 1994). However, in the very cold winter of 1962-3 when temperatures repeatedly fell below 0 °C over a period of 2 months large numbers of *Patella vulgata* were found dead (Crisp, 1964). Periods of frost may also kill juvenile *Patella vulgata*, resulting in recruitment failures in some years (Bowman & Lewis, 1977). In colder conditions an active migration by mobile species found within the turf may occur down the shore to a zone where exposure time to the air (and hence time in freezing temperatures) is less.

Sensitivity assessment. Based on the wide range of temperature tolerance of *Mytilus edulis* and its limited effect on its physiology, it is concluded that the acute and chronic changes described by the benchmarks of 2-5°C would have limited effect. *Fucus vesiculosus* are found in the middle of their natural temperature range in the British Isles and are not considered likely to be affected by a decrease in temperature at the pressure benchmark. Based on the characterizing and associated species, this biotope is considered to have 'High' resistance and 'High resilience (by default) to this pressure and is therefore considered to be 'Not sensitive'. The timing of changes and seasonal weather could result in greater impacts on species. An acute decrease in temperature coinciding with unusually low winter temperatures may exceed thermal tolerances and lead to mortalities of

the associated species although this would not alter the character of the biotope.

Salinity increase (local)

Low

Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Local populations may be acclimated to the prevailing salinity regime and may therefore exhibit different tolerances to other populations subject to different salinity conditions and therefore caution should be used when inferring tolerances from populations in different regions. This biotope is found in full (30-35 ppt) salinity (Connor *et al.*, 2004). Biotopes found in the intertidal will naturally experience fluctuations in salinity where evaporation increases salinity and inputs of rainwater expose individuals to freshwater. Species found in the intertidal are therefore likely to have some form of behavioural or physiological adaptations to changes in salinity.

Mytilus edulis is found in a wide range of salinities from variable salinity areas (18-35 ppt) such as estuaries and intertidal areas, to areas of more constant salinity (30-35 ppt) in the sublittoral (Connor *et al.*, 2004). Furthermore, mussels in rock pools are likely to experience hypersaline conditions on hot days. Newell (1979) recorded salinities as high as 42 psu in intertidal rock pools, suggesting that *Mytilus edulis* can tolerate high salinities.

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

The associated species are typically found in a range of salinities. *Corallina officinalis* is found in tide pools where salinities may fluctuate markedly during exposure to the air. Kinne (1971) cites maximal growth rates for *Corallina officinalis* between 33 and 38 psu in Texan lagoons. *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and is considered to be a very euryhaline species, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979). Laboratory experiments have defined the upper and lethal lower limits for *Palmaria palmata* as 15 psu and 50 psu, (Karsten *et al.*, 2003) with optimal salinity defined as 23-34 psu (Robbins, 1978). The associated *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and are considered to be a very euryhaline, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979). Some variations in salinity tolerance between populations of *Ulva intestinalis* have been found, however, suggesting that plants have some adaptation to the local salinity regime (Alström-Rapaport *et al.*, 2010; Reed & Russell (1979). Increased salinity is most likely to occur in the region of the littoral fringe and supralittoral zone and specimens from these areas were able to tolerate very high salinities, a significant decrease in regeneration only being recorded after exposure to concentrated seawater (102 psu and 136 psu) for > 7 days (Reed & Russell, 1979).

In the laboratory, *Semibalanus balanoides* was found to tolerate salinities between 12 and 50 psu (Foster, 1970). Young *Littorina littorea* inhabit rock pools where salinity may increase above 35 psu. Thus, the associated species may be able to tolerate some increase in salinity.

Sensitivity assessment. Little direct evidence was found to assess sensitivity to this pressure.

Although some increases in salinity may be tolerated by the associated species present these are generally short-term and mitigated during tidal inundation. This biotope is considered, based on distribution of *Mytilus edulis*, *Fucus vesiculosus* and the associated red algal species on the mid to lower shore to be sensitive to a persistent increase in salinity to >40 ppt. Resistance is therefore assessed as 'Low' and recovery as 'Medium' (following restoration of usual salinity). Sensitivity is therefore assessed as 'Medium'.

Salinity decrease (local)

High

Q: High A: High C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: High

Local populations may be acclimated to the prevailing salinity regime and may therefore exhibit different tolerances to other populations subject to different salinity conditions and therefore caution should be used when inferring tolerances from populations in different regions. This biotope is found in full (30-35 ppt) salinity (Connor *et al.*, 2004). Biotopes found in the intertidal will naturally experience fluctuations in salinity where evaporation increases salinity and inputs of rainwater expose individuals to freshwater. Species found in the intertidal are therefore likely to have some form of behavioural or physiological adaptations to changes in salinity.

Mytilus edulis is found in a wide range of salinities from variable salinity areas (18-35 ppt) such as estuaries and intertidal areas, to areas of more constant salinity (30-35 ppt) in the sublittoral (Connor *et al.*, 2004). In addition, *Mytilus edulis* thrives in brackish lagoons and estuaries, although, this is probably due to the abundance of food in these environments rather than the salinity (Seed & Suchanek, 1992). Furthermore, mussels in rock pools are likely to experience hypersaline conditions on hot days. Newell (1979) recorded salinities as high as 42 psu in intertidal rock pools, suggesting that *Mytilus edulis* can tolerate high salinities. Also, *Mytilus edulis* was recorded to grow in a dwarf form in the Baltic sea where the average salinity was 6.5 psu (Riisgård *et al.*, 2013).

Mytilus edulis is an osmoconformer and maintains its tissue fluids iso-osmotic (equal ionic strength) with the surrounding medium by mobilisation and adjustment of the tissue fluid concentration of free amino acids (e.g. taurine, glycine and alanine) (Bayne, 1976; Newell, 1989). But mobilizing amino acids may result in loss of protein, increased nitrogen excretion and reduced growth. However, Koehn (1983) and Koehn & Hilbish (1987) reported a genetic basis to adaptation to salinity. *Mytilus edulis* exhibits a defined behavioural response to reducing salinity, initially only closing its siphons to maintain the salinity of the water in its mantle cavity, which allows some gaseous exchange and therefore maintains aerobic metabolism for longer. If the salinity continues to fall the valves close tightly (Davenport, 1979; Rankin & Davenport, 1981). In the long-term (weeks), *Mytilus edulis* can acclimate to lower salinities (Almada-Villela, 1984; Seed & Suchanek 1992; Holt *et al.*, 1998). Almada-Villela (1984) reported that the growth rate of individuals exposed to only 13 psu reduced to almost zero but had recovered to over 80% of control animals within one month. Observed differences in growth are due to physiological and/or genetic adaptation to salinity.

Decreased salinity has physiological effects on *Mytilus edulis*; decreasing the heart rate (Bahmet *et al.*, 2005), reducing filtration rates (Riisgård *et al.*, 2013), reducing growth rate (Gruffydd *et al.*, 1984) and reducing the immune function (Bussell *et al.*, 2008). Both Bahmet *et al.* (2005) and Riisgård *et al.* (2013) noted that filtration and heart rates return to normal within a number of days acclimation or a return to the original salinity. However, Riisgard *et al.* (2013) did observe that mussels from an average of 17 psu found it harder to acclimate between the salinity extremes than those from an average of 6.5 psu. This observation may mean that mussels in a variable/ lower salinity environment are more able to tolerate change than those found at fully marine salinities. A

sharp salinity change also induces a behavioural response to close the shell (Riisgård *et al.* 2012) to maintain the salinity within the mantle cavity. In extreme low salinities, e.g. resulting from storm runoff, large numbers of mussels may be killed (Keith Hiscock pers comm.). However, Bailey *et al.*, (1996) observed very few mortalities when exposing *Mytilus edulis* to a range of salinities as low as 0 ppt for two weeks at a range of temperatures. It was also noted that there was a fast recovery rate.

Fucus vesiculosus is well adapted to cope with varying salinities and can grow in full saline to brackish conditions. Bäck *et al.* (1992) compared *Fucus vesiculosus* individuals from Atlantic and the Baltic populations. Both populations were able to withstand wide range of salinities in laboratory cultures, yet some differences were recorded. The Atlantic population showed better growth in higher salinities and virtually no growth at 5 ppt. Those individuals kept at 5 ppt mortality occurred after 7 weeks. In contrast the Baltic wracks grew better in conditions with lower salinities, demonstrating that sensitivity of *Fucus vesiculosus* to changes in salinity differ between populations (Bäck *et al.*, 1992).

The associated species are typically found in a range of salinities. *Corallina officinalis* is found in tide pools where salinities may fluctuate markedly during exposure to the air. Kinne (1971) cites maximal growth rates for *Corallina officinalis* between 33 and 38 psu in Texan lagoons. *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and is considered to be a very euryhaline species, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979). Laboratory experiments have defined the upper and lethal lower limits for *Palmaria palmata* as 15 psu and 50 psu, (Karsten *et al.*, 2003) with optimal salinity defined as 23-34 psu (Robbins, 1978). *In-situ Palmaria palmata* from the Arctic Kongsfjord (Spitsbergen) exposed for four days to salinities of 15 psu following freshwater run-off suffered high levels of mortality (Karsten *et al.*, 2003). The associated *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and are considered to be a very euryhaline, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979). Some variations in salinity tolerance between populations of *Ulva intestinalis* have been found, however, suggesting that plants have some adaptation to the local salinity regime (Alström-Rapaport *et al.*, 2010; Reed & Russell (1979). Increased salinity is most likely to occur in the region of the littoral fringe and supralittoral zone and specimens from these areas were able to tolerate very high salinities, a significant decrease in regeneration only being recorded after exposure to concentrated seawater (102 psu and 136 psu) for >7 days (Reed & Russell, 1979). A decrease in salinity may lead to replacement of more sensitive red algal turf forming species by those more tolerant of the changed conditions. *Chondrus crispus* is not characteristic of this biotope but occurs in areas of 'low' salinity. For example, the species occurs in estuaries in New Hampshire, USA, where surface water salinity varies from 16-32 psu (Mathieson & Burns, 1975). Mathieson & Burns (1971) recorded maximum photosynthesis of *Chondrus crispus* in culture at 24 psu, but rates were comparable at 8, 16 and 32 psu. Tasende & Fraga (1999) cultured *Chondrus crispus* spores from north west Spain and concluded that growth was correlated with salinity between 23 and 33 psu.

Semibalanus balanoides are tolerant of a wide range of salinity and can survive periodic emersion in freshwater, e.g. from rainfall or freshwater run-off, by closing their opercular valves (Foster, 1971b). They can also withstand large changes in salinity over moderately long periods of time by falling into a "salt sleep" and can be found on shores (example from Sweden) with large fluctuations in salinity around a mean of 24 (Jenkins *et al.*, 2001). In areas of permanently reduce salinity the Australian barnacle *Austrominius* (formerly *Elminius*) *modestus* may be favoured, as this species is more tolerant of lower salinities), although this is balanced against its lower tolerance of wave exposure. *Littorina littorea* is found in waters of full, variable and reduced salinities (Connor *et al.*,

2004) and so populations are not likely to be highly intolerant of decreases in salinity. Therefore, it appears that the biotope would have low intolerance to a decrease in salinity. On return to normal conditions recovery is likely to be very rapid. *Patella vulgata* can tolerate varying salinities and its distribution extends into the mouths of estuaries surviving in salinities down to about 20 psu. However, growth and reproduction may be impaired in reduced salinity. Little *et al.* (1991), for example, observed reduced levels of activity in limpets after heavy rainfall and in the laboratory activity completely stopped at 12 psu. The species can endure periods of low salinity and was found to die only when the salinity was reduced to 3-1 psu (Fretter & Graham, 1994). In experiments where freshwater was trickled over the shell, Arnold (1957) observed limpets withdrawing and clamping the shell onto the substratum. There appears to be an increasing tolerance of low salinities from the lower to the upper limit of distribution of the species on the shore (Fretter & Graham, 1994).

Sensitivity assessment, Most of the literature found on this topic considered short-term (days to weeks) impacts of changes to salinity whilst the benchmark refers to a change for one year. However, *Mytilus edulis* was shown to be capable of acclimation to changes in salinity. As *Mytilus edulis* is found in salinities to as low as 4-5 psu (Riisgård *et al.*, 2013), it is likely to be able to acclimate to a decrease in salinity at the pressure benchmark. Therefore, *Mytilus edulis* is recorded as having a 'High' resistance to a decrease in salinity and a 'High' resilience (no impact to recover from). Prolonged reduction in salinity, e.g. from full to reduced, is likely to reduce the species richness of the biotope due to loss of less tolerant red algae and some intolerant invertebrates. The sensitivity of *Palmaria palmata* for example, appears to be greater than some other turf-forming species such as *Chondrus crispus*. A change in salinity at the pressure benchmark is considered to lead to some mortality of *Palmaria palmata* although the tolerance threshold reported in laboratory studies is slightly lower than the assessed benchmark. However, the dominant species will probably survive and the integrity of the biotope is likely to be little affected. It is considered that the benchmark decrease in salinity (from full to variable) would not result in mortality of the characterizing species in biotopes that were previously fully marine. Resistance is therefore assessed as 'High' and resilience as 'High', based on no effect to recover from and the biotope is considered to be 'Not sensitive'.

Water flow (tidal current) changes (local)

Medium

Q: High A: High C: Medium

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Blue mussels are active suspension feeders generating currents by beating cilia and are therefore not entirely dependent on water flow to supply food (organic particulates and phytoplankton). Therefore, they can survive in very sheltered areas, but water flow (due to tides, currents or wave action) can enhance the supply of food, carried from outside the area or resuspended into the water column. The evidence for *Mytilus edulis* sensitivity to changes in water flow was reviewed by Mainwaring *et al.* (2014). Individuals attached to solid substrata (rock) as in this biotope are likely to display more resistance than individuals attached to boulders, cobbles or sediment.

The growth rate of *Mytilus edulis* in relation to water flow was investigated by Langan & Howell (1994) who found that the growth rate over 24 days was 0.1, 1.8, 2.0, 1.9 and 1.5 mm at flow rates of 0, 0.01, 0.02, 0.04 and 0.08 m/s respectively. The only growth rate found to be significantly different was at zero flow. However, the pattern did follow that predicted by the 'inhalant pumping speed' hypothesis that suggested maximal growth at water speeds of about 0.02 m/s and decreased growth rates at higher and lower speeds (Langan & Howell 1994). Higher current speed brings food to the bottom layers of the water column, and hence near to the mussels, at a higher

rate (Frechette *et al.*, 1989). Frechette *et al.*, (1989) developed a model based on measurements in the St. Lawrence River estuary (Québec). The model suggested that *Mytilus edulis* consumption rate depends on the flow of water.

Widdows *et al.* (2002) found that there was no change in filtration rate of *Mytilus edulis* between 0.05 and 0.8 m/s. They noted that their finding contradicted earlier work that found a marked decline in filtration rates from 0.05 to 0.25 m/s (Newell, 1999; cited in Widdows *et al.*, 2002) but suggested that the difference might be caused in differences in population studied, as the earlier work was based in the USA and their study used mussels from the Exe estuary in the UK. Widdows *et al.* (2002) also noted that the filtration rate declined above 0.8 m/s mainly because the mussels became detached from the substratum in the experimental flume tank. Widdows *et al.*, (2002) noted that their results were consistent with field observations, as mussels show preferential settlement and growth in areas of high flow, such as the mouth of estuaries and at the base of power station cooling systems (Jenner *et al.*, 1998). They also reported that Jenner *et al.* (1998; cited in Widdows *et al.*, 2002) observed that biofouling of cooling water systems by mussels was only reduced significantly when mean current speeds reached 1.8-2.2 m/s and was absent at >2.9 m/s.

Increased flow rate increases the risk of mussels being detached from the bed and transported elsewhere where their chance of survival will be significantly reduced due to the risk of predation and siltation (Dare, 1976). It is the strength of the byssal attachment that determines the mussel's ability to withstand increases in flow rate. Flow rate itself has been shown to influence the strength and number of byssus threads that are produced by *Mytilus edulis* and other *Mytilus* spp. with mussels in areas of higher flow rate demonstrating stronger attachment (Dolmer & Svane, 1994; Alfaro, 2006). Dolmer & Svane (1994) estimated the potential strength of attachment for *Mytilus edulis* in both still water and flows of 1.94 m/sec, by counting the number of established byssus threads and measuring the strength of attachment of individual detached byssus threads. It was found that in still water the strength of the attachment was 21% of the potential strength whilst at 19.4 cm/sec it was 81 % of the potential strength, suggesting that *Mytilus edulis* has the ability to adapt the strength of its attachment based on flow rate. The mussels were then able to withstand storm surges up to 16 m/s. Young (1985) demonstrated that byssus thread production and attachment increased with increasing water agitation. She observed the strengthening of byssal attachments by 25% within eight hours of a storm commencing and an ability to withstand surges up to 16 m/s. However, it was concluded that sudden surges may leave the mussels susceptible to being swept away (Young, 1985) as they need time to react to the increased velocity to increase the attachment strength. *Mytilus edulis* beds could, therefore, adapt to changes in water flow at the pressure benchmark.

Alfaro (2006) found that when a sudden increase in flow (to 0.13 m/s) was experienced by *Perna canaliculus* (another mussel species) in areas of low flow rate they were more susceptible to detachment than those that had been exposed to a higher flow rate. It was also noted that the individuals kept at higher water flows (e.g. 10 cm/sec) produced more byssus threads. The increased energy used for byssus production in the high flow environments may reduce the energy that is available for other biological activities (Alfaro, 2006).

Water flow also affects the settlement behaviour of larvae. Alfaro (2005) observed that larvae settling in a low water flow environment are able to first settle and then detach and reattach displaying exploratory behaviour before finally settling and strengthening their byssus threads. However, larvae settling in high flow environments did not display this exploratory behaviour. Pernet *et al.*, (2003) found that at high velocities, larvae of *Mytilus* spp. were not able to

exercise much settlement preference. It was thought that when contact with suitable substratum is made the larvae probably secure a firm attachment. Movement of larvae from low shear velocities, where they use their foot to settle, to high shear velocities where they use their byssal thread to settle was observed by Dobretsov & Wahl (2008).

Moderate water movement is beneficial to seaweeds as it carries a supply of nutrients and gases to the plants and removes waste products. Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). Increased water flow can increase scour through increased sediment movement. Small life stages of macroalgae are likely to be affected by removing new recruits from the substratum and hence reducing successful recruitment (Devinny & Vorse, 1978) (see 'siltation' pressures). A reduction in water flow can cause a thicker boundary layer resulting in lower absorption of nutrients and CO₂ by the macroalgae. Slower water movement can also cause oxygen deficiency directly impacting the fitness of algae (Olsenz, 2011). Higher water flow rates increase mechanical stress on macroalgae by increasing drag. This can result in individuals being torn off the substratum. Jonsson *et al.* (2006) found that flow speed of 7-8 m/s completely dislodged *Fucus vesiculosus* individuals larger than 10 cm. Smaller individuals are likely to better withstand increased water flow as they experience less drag. The risk of dislodgement is greater where algae are attached to pebbles instead of bedrock (Isaeus, 2004). As water velocity increases algae can flex and reconfigure to reduce the size of the alga when aligned with the direction of flow, this minimises drag and hence the risk of dislodgement (Denny *et al.*, 1998; Boller & Carrington, 2007). These characteristics allow these species to persist on shores that experience a range of flow speeds. For example, *Mastocarpus stellatus* occurs at sites in Maine, USA experiencing peak Autumn flow speeds as measured by current meters of 9.2 m/s and 5.8 m/s. The habitat structure created by canopies and turfs reduce the effects of water flows on individuals by slowing and disrupting flow (Boller & Carrington, 2006) although this effect will be reduced in this biotope where *Fucus vesiculosus* and red algae occur as scattered plants.

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

Patella vulgata inhabits a range of tidal conditions and is therefore, likely to tolerate a change in water flow rate. The streamlined profile of limpet shells is of importance in increasing their

tolerance of water movement, and this is undoubtedly one factor in determining the different shape of limpets at different exposures. With increasing exposure to wave action the shell develops into a low profile reducing the risk of being swept away. The strong muscular foot and a thin film of mucus between the foot and the rock enables *Patella vulgata* to grip very strongly to the substratum (Fretter & Graham, 1994). The ability of limpets to resist accelerating, as distinct from constant currents, may set a limit to the kind of habitat which they can occupy and limit the size to which they can grow.

Littorina littorea is found in areas with water flow rates from negligible to strong, although populations exposed to different levels of flow may have adapted to local conditions. Increases in water flow rates above 6 knots may cause snails in less protected locations (e.g. not in crevices etc) to be continually displaced into unsuitable habitat so that feeding may become sub-optimal. Thus, populations of *Littorina littorea* are likely to reduce. Shell morphology within littorinids varies according to environmental conditions, in sheltered areas, where *Carcinus maenas* is more prevalent, shell apertures are small to inhibit predation. In exposed areas the foot surface is larger to allow greater attachment and the shell spire is lower to reduce drag (Raffaelli 1982, Crothers, 1992).

Sensitivity assessment. The biotope is characteristic of exposed to moderately wave exposed conditions where water movement from wave action will greatly exceed the strength of any possible tidal flow. Based on the available evidence the characterizing species and associated macroalgae and animals are able to adapt to high flow rates and the biotope is therefore considered to be 'Not sensitive' to an increase in water flow at the pressure benchmark. A decrease in water flow may have some effects on recruitment and growth of filter feeders including *Mytilus edulis*, but this is not considered to be lethal at the pressure benchmark and resistance is therefore assessed as 'High' and resilience as 'High' by default, so that the biotope is considered to be 'Not sensitive'. Changes in water flow at the pressure benchmark may result in increased or decreased sediment deposition, these are not considered to alter the character of the biotope which is silted (Connor *et al.*, 2004) and therefore subject to some scouring but may alter species richness of the small invertebrates associated with the turf. *Patella vulgata* may however be sensitive to increased deposition (see siltation pressures).

Emergence regime changes

Low

Q: High A: High C: High

High

Q: High A: Low C: Medium

Low

Q: High A: Low C: Medium

Emergence regime is a key factor structuring intertidal biotopes. Changes in emergence can lead to; greater exposure to desiccation, temperature and salinity variation, reduced levels of time for filter feeding and nutrient uptake and photosynthesising opportunities for the characterizing species. Changes in emergence can also alter competitive interactions and trophic interactions such as grazing and predation. This biotope occurs in the mid shore (Connor *et al.*, 2004). Typically above this biotope a similar *Mytilus edulis* and *Semibalanus balanoides* dominated biotope (Sem) is found or a *Fucus vesiculosus* dominated biotope (FvesB). In the lower eulittoral zone below MytFves is usually a biotope dominated by the wrack *Fucus serratus*, *Mytilus edulis* and a higher diversity of red seaweeds (MytFR; Fser.R) (Connor *et al.*, 2004).

Mytilus edulis beds are found at a wide range of shore heights from the strandline down to the shallow sublittoral (Connor *et al.*, 2004). Their upper limits are controlled by temperature and desiccation (Suchanek, 1978; Seed & Suchanek 1992; Holt *et al.*, 1998) while the lower limits are set by predation, competition (Suchanek, 1978) and sand burial (Daly & Mathieson, 1977).

Mussels found higher up the shore display slower growth rates (Buschbaum & Saier, 2001) due to the decrease in time during which they can feed and also a decrease in food availability. It has been estimated that the point of zero growth occurs at 55% emergence (Baird, 1966) although this figure will vary slightly depending on the conditions of the exposure of the shore (Baird, 1966; Holt *et al.*, 1998). Increasing shore height does, however, increase the longevity of the mussels due to reduced predation pressure (Seed & Suchanek, 1992; Holt *et al.*, 1998), resulting in a wider age class of mussels found on the upper shore. The lower limit of *Mytilus* beds is mainly set by predation from *Asterias rubens* and *Carcinus maenas* which may increase with a decrease in emergence potentially reducing the lower limit or reducing the number of size classes and age of the mussels at the lower range of the bed (Saier, 2002).

Fucoid dominated biotopes are found in the eulittoral zone and are subjected to cyclical immersion and emersion caused by the tides. During the initial stages of drying, when alga are exposed to air, photosynthetic rates increase due to the higher diffusion rate of CO₂ in air relative to water (Johnson *et al.*, 1974). However this peak in photosynthesis is usually followed by a gradual decline in the rate of photosynthesis as the surface of the alga dries, thereby preventing further dissolution and uptake of CO₂ (Beer & Kautsky 1992). Photosynthesis eventually ceases at a critical state of dehydration when the low water content of the thallus disrupts the functioning of the photosynthetic apparatus (Quadir *et al.* 1979). *Fucus vesiculosus* can tolerate desiccation until the water content is reduced to approx. 30%. If desiccation occurs beyond this level, irreversible damage occurs. Individuals at the top of the shore probably live at the upper limit of their physiological tolerance and are therefore likely to be unable to tolerate increased desiccation and would be displaced by more physiologically tolerant species. Tolerance to this pressure is likely to vary on a geographical scale. Gylle *et al.* (2009) found that *Fucus vesiculosus* populations naturally occurring in fully saline conditions had a higher emersion stress tolerance compared to brackish populations. Early life history stages are more susceptible to this pressure compared to adults (Henry & Van Alstyne, 2004). Germlings are however protected from desiccation by the canopy of adults. A study by Brawley & Johnson (1991) showed that germling survival under adult canopy was close to 100% whereas survival on adjacent bare rock was close to 0% during exposure to aerial conditions.

The red algae within the biotope are likely to be sensitive to increased emergence and to benefit from a decrease. *Corallina officinalis* are sensitive to desiccation (Dommasnes, 1969) and are generally not found on open rock unless protected by algal canopies or where the surfaces are damp or wet. At Hinkley Point (Somerset, England), for example, seawater run-off from deep pools high in the intertidal supports dense turfs of *Corallina* spp. lower on the shore (Bamber & Irving, 1993). Fronds are highly intolerant of desiccation and do not recover from a 15% water loss, which might occur within 40-45 minutes during a spring tide in summer (Wiedemann, 1994). Bleached corallines were observed 15 months after the 1964 Alaska earthquake which elevated areas in Prince William Sound by 10 m. Similarly, increased exposure to air caused by upward movement of 15 cm due to nuclear tests at Armchitka Island, Alaska adversely affected *Corallina pilulifera* (Johansen, 1974). During an unusually hot summer, Hawkins & Hartnoll (1985) observed damaged *Corallina officinalis* and other red algae. Littler & Kauker, (1984) suggest that the basal crustose stage is adaptive, allowing individuals to survive periods of physical stress as well as physiological stress such as desiccation and heating. The basal crust stage may persist for extended periods with frond regrowth occurring when conditions are favourable. The green algae are also resistant to this pressure (although may be bleached at higher shore levels during periods of high temperature) and are found throughout the intertidal including the high shore levels which may not be inundated every day. Experimental grazer removal has allowed algae including *Palmaria palmata*, *Ceramium* sp. and *Osmundea* (as *Laurencia*) *pinnatifida* to grow higher on

the shore (during winter and damp summers) than usual suggesting that grazing also limits the upper shore extent of this biotope. *Palmaria palmata* grew more abundantly higher up the shore following the massive mortality of molluscan grazers after the *Torrey Canyon* oil spill (Hawkins & Hartnoll, 1983).

Mobile epifauna are likely to relocate to more suitable habitats. Species such as *Patella vulgata* and *Littorina littorea* that are found throughout the intertidal zone are adapted to tolerate desiccation to some extent. For example, littorinids can seal the shell using the operculum while limpets clamped tightly to rock will reduce water loss.

Sensitivity assessment. The key characterizing species *Mytilus edulis* is likely to tolerate some increases in emergence as typically a biotope dominated by this species and *Semibalanus balanoides* occurs above this biotope. A significant, long-term, increase in emergence is therefore considered likely to lead to replacement of this biotope with one that is similar but more typical of the changed conditions with less red algae. *Corallina officinalis* and associated red algae are intolerant of desiccation but basal crusts may allow individuals to persist in conditions that are unfavourable to frond development until the emergence regime is re-established. A decrease in emergence is likely to also be tolerated by *Mytilus edulis* but *Fucus serratus* may replace *Fucus vesiculosus* leading to biotope reclassification. As emergence is a key factor structuring the distribution of biotopes on the shore, resistance to a change in emergence (increase or decrease) is assessed as 'Low'. Recovery is assessed as 'High', (based on the impacted *Fucus vesiculosus* and red algae, rather than the unimpacted *Mytilus edulis*) and sensitivity is, therefore, assessed as 'Low'.

Wave exposure changes (local)

High

Q: High A: Medium C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: High

Mytilus edulis are able to increase the strength of their attachment to the substratum in more turbulent conditions (Price, 1982; Young, 1985). Young (1985) demonstrated an increase in strength of the byssal attachment by 25% within 8 hours of a storm commencing. When comparing mussels in areas of high flow rate and low flow rate those at a higher flow rate exhibit stronger attachments than those in the areas of lower flow (Dolmer & Svane, 1994; Alfaro, 2006). Dolmer & Svane (1994) found that in still water the strength of the attachment was 21% of the potential strength whilst at 1.94 m/sec it was 81% of the potential strength. The mussels were then able to withstand storm surges up to 16 m/s. Alfaro (2006) also noted that the individuals kept at higher water flows produce more byssal threads. The increased energy used for byssus production in the high flow environments may reduce the energy that is available for other biological activities (Alfaro 2006). Whilst this clearly demonstrates the ability of mussels to adapt to the various conditions to avoid dislodgement, the mussels are unlikely to adapt instantly and a sudden increase in flow is likely to result in dislodgement (Young, 1985).

Large scale destruction of mussel beds has been reported in many areas such as the Wash, Morecambe Bay and the Wadden Sea (Holt *et al.*, 1998) and it appears that because of this high wave exposure and destruction, reefs found in wave exposed areas are likely to be more dynamic (Nehls & Thiel, 1993). Furthermore, increased wave exposure leads to a higher risk of damage from drift logs (or other flotsam), which once they have destroyed a patch of mussels leave the mussels around that patch at a higher risk of erosion (Seed & Suchanek, 1992). Mussels with high abundance of epizoic and epiphytic (e.g. barnacles and macroalgae) growing on mussels are also more susceptible to removal in areas of high exposure due to increased drag caused by these fouling organisms (Suchanek, 1985; Seed & Suchanek, 1992). However, mussel beds are prevalent

in areas of high wave exposure suggesting a high resilience despite destruction.

Blue mussels display a high resistance to increases in water flow, but the oscillatory water movement that occurs on shores of higher wave exposure is likely to have a higher impact due to the 'to and fro' motion which is more likely to weaken the attachments. Westerbom & Jattu (2006) found that in subtidal mussel beds, mussel densities increased with increasing wave exposure. The highest biomass was found in areas of intermediate exposure, potentially due to the larger mussels being removed at high wave exposure levels. It was suggested that the lower densities found in more sheltered areas were due to low recruitment, early post-recruitment mortality, increased predation or stagnant settlement on rocks. Furthermore, it was also noted that high sedimentation which is more prevalent in sheltered areas, as there is less energy for re-suspension, prevents colonisation and result in the death of small mussels that are living close to the sediment surface by smothering and the clogging up of their feeding apparatus (Westerbom & Jattu, 2006). Therefore, colonization of new space in sheltered areas could be slow, particularly in areas where there is low availability of adult mussels.

An increase in wave exposure may increase density in subtidal beds (Westerbom & Jattu, 2006), unless there is a very sudden storm surge. Mussels on sedimentary substrata are exposed to a higher risk of dislodgement (Widdows *et al.*, 2002). A decrease in wave exposure is likely to result in increased sedimentation and reduced densities (Westerbom & Jattu, 2006) although the risk of dislodgement will be greatly reduced creating more stable beds (Nehls & Thiel, 1993).

The above evidence is variable as different studies have examined beds that differ in habitat, wave exposure, substratum and mussel density. However general trends can be seen. In rocky habitats, increased wave exposure allows mussel to dominate and form beds, especially where the rock surface has a low slope. Where the beds are patchy or damaged (from natural or human activities) they are more susceptible to further damage as a result of wave action or storms (Seed & Suchanek, 1992; Brosnan & Crumrine, 1994). Multi-layered mussel beds are less susceptible to damage, especially where only the surface layer is removed. It has been noted that the build-up of mussel mud (pseudofaeces) under the bed can reduce the attachment of the bed to the underlying substratum. But in areas of wave exposure, the flow of water through the bed will probably prevent the 'mussel mud' accumulating.

An increase in wave exposure generally leads to a decrease in macroalgae abundance and size (Lewis, 1961; Stephenson & Stephenson, 1972; Hawkins *et al.*, 1992; Jonsson *et al.*, 2006). Fucooids are highly flexible but not physically robust and an increase in wave exposure can cause mechanical damage, breaking fronds or even dislodging whole algae from the substratum. Fucooids are permanently attached to the substratum and would not be able to re-attach if removed. Organisms living on the fronds and holdfasts will be washed away with the algae whereas free-living community components could find new habitat in surrounding areas. Wave exposure has been shown to limit size of fucooids (Blanchette, 1997) as smaller individuals create less resistance to waves. *Fucus vesiculosus* have shown to adapt their morphology to wave exposure to help cope with the stress. For instance Bäck (1993) observed shorter individuals with narrow fronds on exposed shores lacking bladders to reduce drag. An alternative coping strategy for wave induced forces is thallus toughening. In the north and the Baltic Sea, thalli from exposed *Fucus vesiculosus* were 30% more resistant to tear and breakage compared to conspecifics from more sheltered sites (Nietsch, 2009). Furthermore, *Fucus vesiculosus* may be better adapted to more exposed positions compared to other fucooids by its ability to regenerate from holdfasts, an ability that *Fucus serratus* lacks (Malm & Kautsky, 2003). As exposure increases the fucooid population will become dominated by small juvenile algae, and dwarf forms of macroalgae which are more

resistant to this pressure. An increase in wave action beyond this would lead to a further increase in the abundance of robust furoids and red seaweeds, such as *Corallina officinalis* (Connor *et al.*, 2004).

A recent study investigated the combined impacts of wave action and grazing on macroalgae distribution (Jonsson *et al.*, 2006). It suggested that recruitment and survival of juvenile *Fucus vesiculosus* is controlled indirectly by wave exposure, through higher limpet densities at exposed locations (Jonsson *et al.*, 2006). A decrease in wave exposure may ultimately reduce *Patella vulgata* abundance because the species does not favour thick algal cover that is often present on more sheltered shores. Alternatively an increase in significant wave height, linked to increased exposure, may result in population changes with fewer macroalgae and with more *Chthamalus* sp. present than *Semibalanus balanoides* (Ballantine, 1961) and the limpet *Patella ulyssiponensis* present, or present in greater numbers, rather than *Patella vulgata* (Thompson, 1980). These changes are not considered to lead to a significant change in biotope character as species replacements are functionally similar.

Sensitivity assessment. The natural wave exposure range of this biotope is considered to exceed changes (increases and decreases) at the pressure benchmark and this biotope is considered to have 'High' resistance and 'High' resilience (by default), to this pressure (at the benchmark). This assessment is supported by evidence for the tolerance and adaptations of the key characterizing *Mytilus edulis* and *Fucus vesiculosus* to different levels of wave exposure. Changes in wave exposure that exceed the pressure benchmark may lead to species replacements and changes in the abundance and density of furoids and red algae but a similar biotope to that described by Connor *et al.* (2004) is likely to remain.

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.

Contamination at levels greater than the benchmark may impact this biotope. The effects of contaminants on *Mytilus* sp. were extensively reviewed by Widdows & Donkin, (1992) and Livingstone & Pipe (1992). Widdows & Donkin (1992) list tolerances of *Mytilus edulis* adults and larvae but note that lethal responses give a false impression of high tolerance, since the adults can close their valves and isolate themselves from the environment for days. They suggested that sublethal effects e.g. shell growth and 'scope for growth' (SFG), are more sensitive indicators of the effects of contaminants. Reported effects of heavy metals follow.

- Adult 15 day LC₅₀ to 50µg/l Cu (Widdows & Donkin, 1992).
- Crompton (1997) reported that adult bivalve mortalities occurred after 4-14 day exposure to 0.1-1 µg/l Hg, 1-10 µg/l Cu and Cd, 10-100 µg/l Zn but 1-10 mg/l for Pb and Ni.
- Widdows *et al.* (1995) reported 'no observed effect thresholds' on feeding or SFG in *Mytilus edulis* tissues of 150 µg Cd/g dry wt, 25 µg Cu/ g dry wt, (lethal at 60 µg Cu/g dry wt), 12 µg Hg/g dry wt, 10 mg Pb/g dry wt, and 300 µg Zn/g dry wt. However, the tissue

concentration of heavy metals at the sites studied was not high enough to reduce SFG significantly.

- Mussels were reported to be missing from an wider area than other shore organisms on a Cumbrian shore in the vicinity of a phosphate rich effluent outfall contaminated by a number of heavy metals (Holt *et al.*, 1998).
- Adults are ca >10 fold more intolerant than larvae to Cu, petroleum hydrocarbons and sewage sludge (Widdows & Donkin, 1992) (see larval sensitivity).

Overall, *Mytilus edulis* is probably relatively tolerant of heavy metal contamination. But the potential mortality indicated above suggest an intolerance of intermediate.

Recovery may occur rapidly through good annual recruitment but examination of patches in beds of *Mytilus* sp. revealed that they may take many years to recover (see additional information below), depending on shore height, competition and environmental conditions. Repeated loss and recruitment results in a patchy distribution of mussels on the shore (Seed & Suchanek, 1992). Therefore, a recoverability of 'high' has been reported.

Little information was found concerning the effects of heavy metals on turf forming and encrusting coralline algae. However, Bryan (1984) suggested that the general order for heavy metal toxicity in seaweeds is: organic Hg > inorganic Hg > Cu > Ag > Zn > Cd > Pb. Most of the information available suggests that the associated adult gastropod molluscs are rather tolerant of heavy-metal toxicity (Bryan, 1984). Littorinids may absorb metals from the surrounding water by absorption across the gills or from their diet, and evidence from experimental studies on *Littorina littorea* suggest that diet is the most important source (Bryan *et al.*, 1983). The species has been suggested as a suitable bioindicator species for some heavy metals in the marine environment. Bryan *et al.* (1983) suggested that the species is a reasonable indicator for Ag, Cd, Pb and perhaps As. In the Fal estuary *Patella vulgata* occurs at, or just outside, Restronguet Point, at the end of the creek where metal concentrations are in the order: Zinc (Zn) 100-2000 µg/l, copper (Cu) 10-100µg/l and cadmium (Cd) 0.25-5µg/l (Bryan & Gibbs, 1983). However, in the laboratory *Patella vulgata* was found to be intolerant of small changes in environmental concentrations of Cd and Zn by Davies (1992). At concentrations of 10µg/l pedal mucus production and levels of activity were both reduced, indicating a physiological response to metal concentrations. Exposure to Cu at a concentration of 100 µg/l for one week resulted in progressive brachycardia (slowing of the heart beat) and the death of limpets. Zn at a concentration of 5500 µg/l produced the same effect (Marchan *et al.*, 1999).

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.

Contamination at levels greater than the benchmark may impact this biotope. Widdows & Donkin (1992) list tolerances of *Mytilus edulis* adults and larvae but note that lethal responses give a false impression of high tolerance, since the adults can close their valves and isolate themselves from the environment for days. They suggested that sublethal effects e.g. shell growth and 'scope for growth' (SFG), are more sensitive indicators of the effects of contaminants.

- Widdows *et al.* (1995) demonstrated that toxic hydrocarbons, primarily poly-aromatic hydrocarbons, made a large contribution the decline in SFG observed along the North Sea coast. Hydrocarbons reduce clearance rate through 'non-specific narcosis'.

- Mussel populations in Sullom Voe experienced moderate hydrocarbon pollution and a reduced SFG but had sufficient capacity to grow, reproduce and maintain a viable population (Widdows *et al.*, 1987).
- Widdows *et al.* (1987) examined the response of *Mytilus edulis* to high oil (water accommodated fraction of diesel oil) ($125 \pm 28 \mu\text{g/l}$) and low oil ($28 \pm 7 \mu\text{g/l}$) over a 8 month period, and subsequent recovery. They observed a marked reduction in SFG (due to reduced feeding rate and food absorption efficiency), and a correlation between the reduction in SFG and the hydrocarbon tissue burden (Widdows *et al.*, 1987; Widdows & Donkin, 1992; Widdows *et al.*, 1995). Mussels exposed to high oil conditions showed a negative SFG and weight loss. During recovery, 22 days after removal to 'clean' seawater the high oil mussels depurated (removed) hydrocarbons more rapidly than low oil mussels, and showed an increased clearance rate and growth rate associated with 'catch-up' growth. Both high and low oil mussels recovered completely within 55 days.
- Widdows *et al.* (1987) also reported that high and low oil contamination of the experimental basins resulted in 100% mortality amongst mussels kept in the basins from autumn 1982 to summer 1983 and from spring 1983 to summer 1984 respectively.
- A sunflower oil tanker spill off the Anglesey coast resulted in ingestion of oil droplets and subsequent mortalities after spawning (Mudge *et al.*, 1993; Holt *et al.*, 1998).
- Bokn *et al.*, (1993) demonstrated that *Mytilus edulis* was lost from mesocosm experiments continuously dosed with 30.1 to 129.4 $\mu\text{g/l}$ of the water accommodated fraction of diesel, and was the most intolerant of the intertidal species studied.
- *Mytilus edulis* dominated jetty piles immediately adjacent to an oil refinery effluent in Milford Haven, suggesting a high tolerance of hydrocarbon contamination (K. Hiscock, pers. comm.).

Overall, hydrocarbon tissue burden results in decreased SFG and in some circumstances may result in mortalities, reduced abundance or extent of *Mytilus edulis*.

Following the *Torrey Canyon* oil spill in 1967, oil and detergent dispersants affected high shore specimens of *Corallina officinalis* more than low shore specimens. Plants in deep pools were afforded some initial protection, although probably later affected by contaminated runoff. In areas of heavy spraying, however, *Corallina officinalis* was killed (Smith 1968). Intolerance to hydrocarbon pollution has been assessed to be high, as key structural and important characterizing coralline algal species will be lost and the biotope not be recognized in their absence. Hydrocarbon contamination, at levels greater than the benchmark, e.g. from spills of fresh crude oil or petroleum products, may cause significant loss of *Ulva* spp. However, the species tends to recover very rapidly from oil pollution incidents. For instance, after the *Torrey Canyon* tanker oil in 1967, grazing species were killed, and a dense flush of ephemeral green algae (*Ulva*, *Blidingia*) appeared on the rocky shore within a few weeks and persisted for up to one year (Smith, 1968).

In areas of moderate oil deposit, up to about 1/2cm thick, on rocks after the *Torrey Canyon* oil spill, limpets had survived unscathed over a month after the event and feeding continued even though a coating of oil smothered their food source of algae and diatoms (Smith, 1968). Limpets can ingest thick oil and pass it through their gut. However, thick layers of oil smothering individuals will interfere with respiration and spoil normal food supplies for *Patella vulgata*. After the *Braer* oil spill, in common with many other oil spills, the major impact in the intertidal zone was on the population of limpets and other grazers. In West Angle Bay, where fresh oil from the *Sea Empress* tanker reached rocky shores within one day of the spill, limpet mortality was 90% (Glegg *et al.*, 1999). Thus *Patella vulgata* has higher intolerance to fresh oil which has a high component of volatile

hydrocarbons remaining. A significant reduction in the density of juvenile limpets was also observed at all sites known to have been oiled by the *Sea Empress* spill (Moore, 1997). In longer term studies into the environmental effects of oil refinery effluent discharged into Littlewick Bay, Milford Haven, the number of limpets, usually found in substantial numbers on this type of shore, were considerably reduced in abundance on areas close to the discharge (Petpiroon & Dicks, 1982). In particular only large individuals were found close to the outfall point and juveniles were completely absent, suggesting that observed changes in abundance resulted from effluent effects on larval stages rather than upon adults directly.

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.

Contamination at levels greater than the benchmark may impact this biotope. The effects of contaminants on *Mytilus* sp. were extensively reviewed by Widdows & Donkin, (1992) and Livingstone & Pipe (1992). Mussels are suspension feeders and, therefore, process large volumes of water together with suspended particulates and phytoplankton. Mussels absorb contaminants directly from the water, through their diet and via suspended particulate matter (Widdows & Donkin, 1992), the exact pathway being dependant on the nature of the contaminant.

- Widdows and Donkin (1992) reported 50% mortality from a tissue burden of 20 µg/g TBT.
- Exposure of *Mytilus edulis* to detergent (BP1002) in seawater resulted in 100% mortality at 10 ppm detergent, although all survived at 5 ppm detergent (Smith, 1968).
- Liu & Lee (1975) reported a LC₅₀ of 250 µg/l of the herbicide trifluralin in *Mytilus galloprovincialis*
- *Mytilus edulis* has been reported to bioaccumulate the insecticide ivermectin, although no adverse effects were observed (Cole *et al.*, 1999).
- Biphenyl (a dye carrier) reduced the feeding rate of *Mytilus edulis* by 50% at 0.3 mg/l (Donkin *et al.*, 1989).
- PCBs accumulate in gonads, although tissue concentrations are significantly reduced after spawning, although this may affect the next generation (Hummel *et al.*, 1989; Holt *et al.*, 1995).
- Significant increases in the incidence of tumours (neoplasia) were reported in the US Mussel Watch programme in the presence of higher concentrations of combustion related poly-aromatic hydrocarbons, *cis*-chlordane pesticides and cadmium (Hillman, 1993; Holt *et al.*, 1998).
- *Mytilus edulis* survived in a power station cooling water culvert, exposed to 0.1-0.2 mg/l hypochlorite, although their growth rates were reduced by about a third. Mussels were able to recover in hypochlorite free periods between chlorination dosing (Thompson *et al.*, 1997). *Mytilus edulis* and *Mytilus galloprovincialis* were reported to suffer 100% mortality after 15-135 days continuous exposure to 0.2-1.0 mg/l hypochlorite (Khalanski & Borget, 1980; cited in Thompson *et al.*, 1997).
- Holt *et al.* (1995) also report that mussels may be absent from areas of high boating activity, presumably due to TBT.

Widdows *et al.* (1995) compared 'scope for growth' (SFG) and chemical contaminants in tissues of mussels from 26 coastal and 9 offshore sites around the United Kingdom. They noted that polar organics (probably derived from phytoplankton) accounted for some reduction in SFG, while

organo-chlorides showed a significant correlation with an unexplained component of the decline in SFG. However, TBT levels were only high enough to cause an effect (<10% reduction in SFG) at 8 study sites (Widdows *et al.*, 1995). *Mytilus edulis* is probably relatively tolerant of contaminants. Widdows & Donkin (1992) list tolerances of *Mytilus edulis* adults and larvae (but note that lethal responses give a false impression of high tolerance, since the adults can close their valves and isolate themselves from the environment for days. They suggest that sublethal effects (shell growth and 'scope for growth') are more sensitive indicators of the effects of contaminants. Also, adults are ca. 4 times more sensitive than larvae to TBT (Widdows & Donkin, 1992, see larval sensitivity).

Following the *Torrey Canyon* oil spill in 1967, oil and detergent dispersants affected high shore specimens of *Corallina officinalis* more than low shore specimens. Plants in deep pools were afforded some initial protection, although probably later affected by contaminated runoff. In areas of heavy spraying, however, *Corallina officinalis* was killed. (Smith 1968). Limpets are extremely intolerant of aromatic solvent based dispersants used in oil spill clean-up. During the clean-up response to the *Torrey Canyon* oil spill nearly all the limpets were killed in areas close to dispersant spraying. Viscous oil will not be readily drawn in under the edge of the shell by ciliary currents in the mantle cavity, whereas detergent, alone or diluted in seawater, would creep in much more readily and be liable to kill the limpet (Smith, 1968). A concentration of 5ppm killed half the limpets tested in 24 hours (Southward & Southward, 1978; Hawkins & Southward, 1992). Acidified seawater affects the motility of *Patella vulgata*. At a pH of 5.5 motility was reduced whilst submerged but individuals recovered when returned to normal seawater. At a pH of 2.5 total inhibition of movement occurred and when returned to normal seawater half had died (Bonner *et al.*, 1993). Reduced motility reduces time for foraging and may result in decreased survival of individuals. Acidified seawater can also change the shell composition which will lead to a decrease in its protective nature and hence survival (Bonner *et al.*, 1993). Short periods (48 hours) are unlikely to have much effect on a population but long periods (1 year) may cause reduced grazing and an increase in algal growth. However, seawater is unlikely to reach pH 2.5 therefore intolerance to slight changes in pH will be low. Hoare & Hiscock (1974) reported that in Amlwch Bay *Patella vulgata* was excluded from sites within 100-150m of the discharge of acidified, halogenated effluent.

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

The periostracum of *Mytilus edulis* was reported to concentrate uranium (Widdows & Donkin, 1992). Mussels have also been reported to bioaccumulate ¹⁰⁶Ru, ⁹⁵Zr, ⁹⁵Nb, ¹³⁷Cs and ⁹⁰Sr (Cole *et al.*, 1999). Algae bioaccumulate radionuclides (with extent depending on the radionuclide and the algae species). Adverse effects have not been reported at low levels. While the above data demonstrates that *Mytilus edulis* can accumulate radionuclides, little information concerning the effects of radionuclides on marine organisms was found. Therefore sensitivity was not assessed based on lack of 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: High A: High C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: Medium

This biotope would only be exposed to low oxygen in the water column intermittently during periods of tidal immersion. In addition, in areas of wave exposure and/or moderately strong current flow, low oxygen levels in the water are unlikely to persist for very long as oxygen levels will be recharged by the incorporation of oxygen in the air into the water column or flushing with oxygenated waters.

Mytilus edulis is regarded as euryoxic, tolerant of a wide range of oxygen concentrations including zero (Zandee *et al.*, 1986; Wang & Widdows 1991; Gosling, 1992; Zwaan de & Mathieu 1992; Diaz & Rosenberg 1995; Gray *et al.*, 2002). Diaz & Rosenberg (1995) suggest it is resistant to severe hypoxia. Adult mytilids exhibited high tolerance of anoxia in laboratory tests, e.g. Theede *et al.*, (1969) reported LD50 of 35 days for *Mytilus edulis* exposed to 0.21 mg/l O₂ at 10°C, which was reduced to 25 days with the addition of sulphide (50 mg/l Na₂S.9H₂O). Jorgensen (1980) observed, by diving, the effects of hypoxia (0.2 - 1 mg/l) on benthic macrofauna in marine areas in Sweden over a 3-4 week period. Mussels were observed to close their shell valves in response to hypoxia and survived for 1-2 weeks before dying (Cole *et al.*, 1999; Jorgensen, 1980). All life stages show high levels of tolerance to low oxygen levels. *Mytilus edulis* larvae, for example, are tolerant down to 1.0 ml/l, and although the growth of late stage larvae is depressed in hypoxic condition, the settlement behaviour does not seem to be affected (Diaz & Rosenberg, 1995). Based on the available evidence *Mytilus edulis* are considered to be resistant to periods of hypoxia and anoxia although sub-lethal effects on feeding and growth may be expected.

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

Experiments have shown that thallus discs of *Ulva lactuca* plants can survive prolonged exposure to anoxia and hypoxia (Vermaat & Sand-Jensen, 1987; Corradi *et al.*, 2006). Following resumption of normal oxygen conditions gametes were produced. The associated invertebrate species also show high tolerances for reduced oxygen at levels that exceed the pressure benchmark. *Littorina littorea* can easily survive 3-6 days of anoxia (Storey *et al.*, 2013). *Semibalanus balanoides* can respire anaerobically, so they can tolerate some reduction in oxygen concentration (Newell, 1979). When placed in wet nitrogen, where oxygen stress is maximal and desiccation stress is low, *Semibalanus balanoides* have a mean survival time of 5 days (Barnes *et al.*, 1963). Limpets can also survive for a short time in anoxic seawater; Grenon & Walker, (1981) found that in oxygen free water limpets could survive up to 36 hours, although Marshall & McQuaid (1989) found a lower tolerance for *Patella granularis*, which survived up to 11 hours in anoxic water. *Patella vulgata* and *Littorina littorea* are able to respire in air, mitigating the effects of this pressure during the tidal cycle.

Sensitivity assessment *Mytilus edulis* is considered to be 'Not Sensitive' to de-oxygenation at the pressure benchmark and the assessment is largely based on this species. As the biotope will only be exposed to this pressure when emersed and wave action will re-oxygenate waters while respiration will occur in air, biotope resistance was assessed as 'High' and resilience as 'High'

(no effect to recover from), resulting in a sensitivity of 'Not sensitive'.

Nutrient enrichment

High

Q: High A: High C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: High

This pressure relates to increased levels of nitrogen, phosphorus and silicon in the marine environment compared to background concentrations. The benchmark is set at compliance with WFD criteria for good status, based on nitrogen concentration (UKTAG, 2014).

Nutrient enrichment may impact mussel beds by altering the biomass of phytoplankton and macroalgae. At low levels, nutrient enrichment may stimulate the growth of phytoplankton used as food - a potential beneficial effect. In the Wadden Sea, where fishing had caused the destruction of the local population of *Sabellaria spinulosa*, *Mytilus edulis* was able to colonize, partly because of the increase in coastal eutrophication (Maddock, 2008). Conversely, Dinesen *et al.* (2011) observed that a reduction in nutrient loading to comply with the WFD resulted in a decrease of mussel biomass in estuaries.

High levels of enrichment may stimulate algal blooms and macroalgal growth. The growth of macrophytes on the mussel beds may result in increased drag on the mussel bed and hence increase susceptibility to damage from wave action and/or storms (see changes in wave exposure pressure). Algal blooms may die off suddenly, causing de-oxygenation (see de-oxygenation pressure) where the algae decompose on the seabed. The thresholds at which these blooms occur depend on site-specific conditions and be mitigated by the degree of mixing and tidal exchange. Some algae have been shown to negatively affect *Mytilus edulis* when present in high concentrations. For example, blooms of the algae *Phaeocystis* sp., have been observed to block the mussels gills when present in high concentrations reducing clearing rates, and at high levels they caused a complete cessation of clearance (Smaal & Twisk, 1997). Blockage of the gills is also likely to reduce ingestion rates, prevent growth and cause reproductive failure (Holt *et al.*, 1998). Other species known to negatively impact *Mytilus edulis* are *Gyrodinium aureolum* (Tangen, 1977; Widdows *et al.*, 1979b) and non-flagellated chrysophycean alga (Tracey, 1988). The accumulation of toxins from algal blooms has also been linked to outbreaks of paralytic shellfish poisoning resulting in the closure of shell fish beds (Shumway, 1990).

The red alga *Corallina officinalis* and the associated green algae species have been identified worldwide as species that occur in areas subject to increased nutrient input within the vicinity of sewage outfalls and at intermediately polluted sites (Bellgrove *et al.*, 2010; Littler & Murray, 1975; May, 1985; Brown *et al.*, 1990; Bellgrove *et al.*, 1997). For example, Kindig & Littler (1980) demonstrated that *Corallina officinalis* var. *chilensis* in South California showed equivalent or enhanced health indices, highest productivity and lowest mortalities (amongst the species examined) when exposed to primary or secondary sewage effluent. Grazers in the biotope may also benefit from increased availability of food resources, due to enhanced growth.

Atalah & Crowe (2010) added nutrients to rockpools occupied by a range of algae including encrusting corallines, turfs of *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina officinalis* and green and red filamentous algae. The invertebrates present were mostly *Patella ulyssiponensis*, the winkle *Littorina littorea* and the flat top shell *Gibbula umbilicalis*. Nitrogen and phosphorous enhancement was via the addition of fertilizers, as either 40 g/litre or 20 g/litre. The treatments were applied for seven month and experimental conditions were maintained every two weeks. The experimental treatments do not directly relate to the pressure benchmark but indicate some general trends in sensitivity. Nutrients had no significant effect on the cover of *Corallina officinalis*.

The cover of green filamentous algae was significantly increased both by reduced grazing and increased nutrients, although the effect size was synergistically magnified by the combined effect of grazer removal and nutrients. Nutrient enrichment caused an absolute increase in the average cover of green filamentous algae of 19% (± 3.9 S.E.) respect to the control treatments while the cover of red turfing algae was not affected by nutrient addition (Atalah & Crowe, 2010).

Sensitivity assessment. The pressure benchmark is relatively protective and may represent a reduced level of nutrient enrichment in previously polluted areas. *Mytilus edulis* beds are considered to be 'Not sensitive' to nutrient enrichment at levels that comply with the requirements for good status for transitional and coastal water bodies (UKTAG, 2014). Due to the tolerance of high levels of nutrient input demonstrated generally e.g. Bellgrove *et al.*, (2010) and Atalah & Crowe, (2010), resistance to this pressure is assessed as 'High' and resilience as 'High' so that the biotope is assessed as 'Not sensitive'. Where *Corallina* dominated biotopes have replaced canopy forming species in enriched areas it is not clear whether a change to the benchmark would lead to a shift in biotope type. Once established the presence of *Corallina* spp. and other turf forming species may limit recruitment by taller species (Bellgrove *et al.*, 2010). No evidence was found to support an assessment of this indirect effect and it is not presented within the table.

Organic enrichment

High

Q: High A: Medium C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: High

Organic enrichment can result from inputs of additional organic matter. It should be noted that biotopes occurring in tide swept or wave exposed areas are less likely to experience the effects of organic enrichment as the organic matter will be rapidly removed. It has been demonstrated that regardless of the concentration of organic matter *Mytilus edulis* will maintain its feeding rate by compensating with changes to filtration rate, clearance rates, production of pseudofaeces and absorption efficiencies (Tracey, 1988; Bayne *et al.*, 1993; Hawkins *et al.*, 1996). A number of studies have highlighted the ability of *Mytilus edulis* to utilise the increased volume of organic material available at locations around salmon farms. Reid *et al.*, (2010) noted that *Mytilus edulis* could absorb organic waste products from a salmon farm with great efficiency. Increased shell length, wet meat weight, and condition index were shown at locations within 200m from a farm in the Bay of Fundy allowing a reduced time to market (Lander *et al.*, 2012). *Mytilus edulis* have also been recorded in areas around sewage outflows (Akaishi *et al.*, 2007; Lindahl & Kollberg, 2008; Nenonen *et al.*, 2008; Giltrap *et al.*, 2013) suggesting that they are highly tolerant of the increase in organic material that would occur in these areas.

Organic enrichment and nutrient enrichment commonly co-occur, for example sewage deposits or outputs from fish farms may enhance nitrogen and phosphorous and organic matter. Major declines of *Fucus vesiculosus* have been reported from all over the Baltic Sea associated with eutrophication from nutrient enrichment (Kautsky *et al.*, 1986). Nutrient enrichment alters the selective environment by favouring fast growing, ephemeral species such as *Ulva lactuca* and *Ulva intestinalis* (Berger *et al.*, 2004, Kraufvelin, 2007). Rohde *et al.*, (2008) found that both free growing filamentous algae and epiphytic microalgae can increase in abundance with nutrient enrichment. This stimulation of annual ephemerals may accentuate the competition for light and space and hinder perennial species development or harm their recruitment (Berger *et al.*, 2003; Kraufvelin *et al.*, 2007). Nutrient enrichment can also enhance fouling of *Fucus* fronds by biofilms (Olsenz, 2011). Nutrient enriched environments can not only increase algae abundance, but the abundance of grazing species (Kraufvelin, 2007). High nutrient levels may directly inhibit spore settlement and hinder the initial development of *Fucus vesiculosus* (Bergström *et al.*, 2003). Bellgrove *et al.* (2010)

found that coralline turfs out-competed fucoids at a site associated with organic enrichment caused by an ocean sewage outfall. Worldwide *Corallina officinalis* has been noted to increase at the expense of canopy forming macroalgae within the vicinity of sewage outfalls and at intermediately polluted sites (Belgrove *et al.*, 2010; Littler & Murray, 1975; May, 1985; Brown *et al.*, 1990). As turf forming algae *Corallina* spp. trap large amounts of sediment and are therefore not considered sensitive to sedimentation. The turfs host a variety of associated species and deposit feeders amongst these would be able to consume inputs of organic matter.

Cabral-Oliveira *et al.*, (2014), found higher abundances of juvenile *Patella* sp. and lower abundances of adults closer to sewage inputs, Cabral-Oliveira *et al.*, (2014) suggested the structure of these populations was due to increased competition closer to the sewage outfalls.

Sensitivity assessment. Based on resistance to sedimentation, exposure to wave action and observations of *Mytilus edulis* and turf forming algae thriving in areas of increased organic matter (Lander *et al.*, 2012, Reid *et al.*, 2010), it was considered that this biotope had 'High' resistance to increased organic matter at the pressure benchmark (which represents enrichment rather than gross pollution). Resilience is therefore assessed as 'High' (no effect to recover from) and the biotope is considered to be 'Not sensitive'.

A Physical Pressures

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

All marine habitats and benthic species are considered to have a resistance of 'None' to this pressure and to be unable to recover from a permanent loss of habitat (resilience is 'Very Low'). Sensitivity within the direct spatial footprint of this pressure is, therefore 'High'. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure. Adjacent habitats and species populations may be indirectly affected where meta-population dynamics and trophic networks are disrupted and where the flow of resources e.g. sediments, prey items, loss of nursery habitat etc. is altered.

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

This biotope is characterized by the hard rock substratum to which the characterizing *Mytilus edulis*, *Fucus vesiculosus* and associated species such as red and green algae, barnacles limpets and anemones can firmly attach. A change to a sedimentary substratum would significantly alter the character of the biotope and would lead to the development of a biological assemblage more typical of the changed conditions. A change to an artificial substratum could also impact the development of this biotope as species may have settlement preferences for particular surface textures. *Mytilus edulis* can be found on a wide range of substrata including artificial substratum (e.g. metal, wood, concrete), bedrock, biogenic reef, caves, crevices / fissures, large to very large boulders, mixed, muddy gravel, muddy sand, rock pools, sandy mud, small boulders, under boulders (Connor *et al.*, 2004). An increase in the availability of hard substratum may be beneficial in areas where sedimentary habitats were previously unsuitable for colonisation e.g. coarse, mobile sediments. However, artificial hard substratum may also differ in other characteristics from

natural hard substratum, so that replacement of natural surfaces with artificial may lead to changes in the biotope through changes in species composition, richness and diversity (Green *et al.*, 2012; Firth *et al.*, 2014) or the presence of non-native species (Bulleri & Airoidi, 2005). *Corallina officinalis* shows optimal settlement on finely rough artificial substrata (0.5 - 1 mm surface particle diameter). Although spores will settle and develop as crustose bases on smooth surfaces, fronds were only initiated on rough surfaces. *Corallina officinalis* settled on artificial substrata within one week in the field in summer months in New England (Harlin & Lindbergh 1977). However, in the laboratory fronds can grow from bases attached to smooth surfaces (Wiedeman pers comm. previous MarLIN review). Similarly, tests with stone panels fixed to the sublittoral, mid-tide and high-tide levels of varying roughness found that *Ulva* (as *Enteromorpha*) species settle preferentially on smoother, fine-grained substratum (chalk, mottled sandstone) and *Porphyra purpurea* on rougher, granulated substratum (limestone, granite, basaltic larvae) (Luther, 1976).

Changes in substratum type can also lead to indirect effects. For example, Shanks & Wright (1986) observed that limpet mortalities were much higher at sites where the supply of loose cobbles and pebbles were greater, leading to increased abrasion through wave action 'throwing' rocks onto surfaces. Littorinids are found on a variety of shores, including sedimentary so a change in type may not significantly affect this species and some of the invertebrate species such as nematodes, amphipods and oligochaetes and polychaetes associated with sediments trapped in the *Corallina* turf are also found in sedimentary habitats

Sensitivity assessment. A change to a soft sedimentary habitat would remove the habitat for this biotope, resistance is assessed as 'None' and resilience as 'Very Low' as the change is considered to be permanent. Sensitivity is therefore assessed as 'High'.

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 occurring on bedrock.

Habitat structure changes - removal of substratum (extraction)

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

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

Abrasion/disturbance of the surface of the substratum or seabed

Low

Q: High A: Medium C: Medium

Medium

Q: High A: High C: High

Medium

Q: High A: Medium C: Medium

The species characterizing this biotope occur on the rock and, therefore, have no shelter from abrasion at the surface. *Mytilus edulis* lives on the surface of the seabed held by byssus threads attached to either the substratum or to other mussels in the bed. Activities resulting in abrasion and disturbance can either directly affect the mussel by crushing them or indirectly affect them by the weakening or breaking of their byssus threads making them vulnerable to displacement (Denny, 1987) where they are unlikely to survive (Dare, 1976). In addition, abrasion and sub-

surface damage may attract mobile scavengers and predators including fish, crabs, and starfish to feed on exposed, dead and damaged individuals and discards (Kaiser & Spencer, 1994; Ramsay *et al.*, 1998; Groenewold & Fonds, 2000; Bergmann *et al.*, 2002). This effect will increase predation pressure on surviving damaged and intact *Mytilus edulis*. A number of activities or events that result in abrasion and disturbance and their impacts on mussel beds are described below, based on the review by Mainwaring *et al.* (2014).

In general, studies have found that trampling is an additional disturbance to the natural disturbances that the intertidal organisms are adapted to tolerate. Large declines of *Mytilus californianus* from mussel beds due to trampling have been reported (Brosnan, 1993; Brosnan & Crumrine, 1994; Smith & Murray, 2005). Brosnan & Crumrine (1994) recorded the loss of 54% of mussels from a single experimental plot on one day. Mussels continued to be lost throughout the experimental period, forming empty patches larger than the experimental plots. The empty patches continued to expand after trampling had ceased, due to wave action. At another site, the mussel bed was composed of two layers, so that while mussels were lost, cover remained. Brosnan (1993) also reported a 40% loss of mussels from mussel beds after three months of trampling and a 50% loss within a year. Van de Werfhorst & Pearse (2007) examined *Mytilus californianus* abundance at sites with differing levels of trampling disturbance. The highest percentage of mussel cover was found at the undisturbed site while the severely disturbed site showed low mussel cover. Brosnan and Crumrine (1994) noted that mussels that occupied hard substrata but did not form beds were also adversely affected. Although only at low abundance (2.5% cover), all mussels were removed by trampling within 4 months. Brosnan & Crumrine (1994) noted that mussels were not common and confined to crevices in heavily trampled sites. Similarly, the mussel bed infauna (e.g. barnacles) was adversely affected and were crushed or lost with the mussels to which they were attached. However, Beauchamp & Gowing (1982) did not observe any differences in mussel density between sites that differed in visitor use.

Smith & Murray (2005) examined the effects of low-level disturbance on an extensive bed of *Mytilus californianus* (composed of a single layer of mussels) in southern California. Smith & Murray (2005) reported that in experimental plots exposed to trampling, mussel loss was 20-40% greater than in untreated plots. A decrease in mussel mass, density, cover and maximum shell length were recorded even in low intensity trampling events (429 steps/m²). However, only 15 % of mussel loss was as a direct result of trampling, with the remaining loss occurring during intervals between treatment applications. Brosnan & Crumrine (1994) suggested that trampling destabilizes the mussel bed, making it more susceptible to wave action, especially in winter. Smith & Murray (2005) suggested that an indirect effect of trampling was weakening of byssal threads, which increases mussel susceptibility to wave disturbance (Denny, 1987). Brosnan & Crumrine (1994) observed recruitment within experimental plots did not occur until after trampling had ceased, and no recovery had occurred within 2 years

Paine & Levine (1981) examined natural patch dynamics in a *Mytilus californianus* bed in the USA. They suggested that it may take up to seven years for large barren patches to recover. However, chronic trampling may prevent recovery altogether. This would result in a shift from a mussel dominated habitat to one dominated by an algal turf or crust (Brosnan & Crumrine, 1994), completely changing the biotope. However, a small period of trampling could allow communities to recover at a similar rate to that of natural disturbance as the effects are similar. The associated epifauna and epiflora suffer the greatest amount of damage as they are the first organisms that a foot makes contact with (Brosnan & Crumrine, 1994). The loss of epifauna and epiflora could initially be of benefit to the mussel bed, despite the obvious decrease in species diversity, as there will be a decrease in drag for the mussels reducing the risk of dislodgement (Witman & Suchanek

1984) and freeing up more energy for growth and reproduction. However, it is likely that after continued trampling this effect will be minimal compared with the increased risk of dislodgement caused by trampling. No studies assessing the effect of trampling on mussels on intertidal muddy sand or sediments were found. Losses to the adult mussels by crushing or by suffocation where these are forced into the sediment are expected. There is the potential that this will open up areas for new recruitment or it may just create a similar situation to that seen on the rocky shore where wave damage and continual trampling prevent settlement and recovery.

The collision of objects with the bed, such as wave driven logs (or similar flotsam), is known to cause the removal of patches of mussels from mussel beds (Seed & Suchanek, 1992; Holt *et al.*, 1998). When patches occur in mussel beds a good recruitment could result in a rapid recovery or the patch may increase in size through the weakening of the byssus threads of the remaining mussels leaving them vulnerable to erosion from storm damage (Denny, 1987). Damage in areas of high wave exposure is likely to result in increased erosion and a patchy distribution although recruitment may be high. In sheltered areas, damage may take a lot longer due to limited larval supply, although the frequency of destruction through wave driven logs would be less than in high wave exposure. Similar effects could be observed through the grounding of a vessel, the dropping of an anchor or the laying of a cable, although the scale of damage clearly differs. Shifting sand is known to limit the range of *Mytilus edulis* through burial and abrasion (Daly & Mathieson, 1977).

Little & Little (1984) suggest that the basal crustose stage of *Corallina officinalis* is adaptive to resist sand scour and wave shearing (as well as physiological stressors such as desiccation and heating). The base is much tougher than the fronds shown by experiments that demonstrate that the base has nearly twice the mechanical resistance (measured by penetration) of fronds (Little & Kauker, 1984). In general, studies show that *Corallina* and other turf forming algae appear to be relatively resistant to single events and low levels of trampling. Brosnan & Crumrine (1994), for example, found that in experimentally trampled plots the cover of foliose and canopy forming species declined while turf forming algae were relatively resistant. Similarly, a comparison of rocky intertidal ledges that received different amounts of visitors in Dorset, England, found that *Corallina officinalis* were present on both heavily visited and less visited ledges suggesting that this species has some resistance to trampling (Pinn & Rodgers, 2005). Povey & Keough (1991) in Mornington Peninsula, Australia investigated the effects of sustained trampling on intertidal coralline algal mats, where upright branching *Corallina* spp. formed a turf with other red algae with sand and encrusting coralline algae between turfs. The experimental strips were 2 m long and 0.5 m wide. The percentage cover of upright *Corallina* spp. was significantly affected by 25 passages of a strip per day after 12 and 33 days. The algae appeared flattened and were shorter (1-2 cm high) compared with the low intensity and control plots (3-4 cm high). However, low-intensity trampling within a strip (2 passages/ day) did not significantly affect the coralline turf. Brown & Taylor (1999) found that higher intensities of trampling damaged turfs. Moderate (50 steps per 0.09 m²) or more trampling on intertidal articulated coralline algal turf in New Zealand reduced turf height by up to 50 %, and weight of sand trapped within turf to about one-third of controls. This resulted in declines in densities of the meiofaunal community within two days of trampling. Although the community returned to normal levels within 3 months of trampling events, it was suggested that the turf would take longer to recover its previous cover (Brown & Taylor, 1999). Similarly, Schiel & Taylor (1999) noted that trampling had a direct detrimental effect on coralline turf species on the New Zealand rocky shore. At one site coralline bases were seen to peel from the rocks (Schiel & Taylor, 1999), however, this was probably due to increased desiccation caused by loss of the algal canopy.

Ulva spp. fronds are very thin and could be torn and damaged and individuals may be removed

from the substratum, altering the biotope through changes in abundance and biomass. *Ulva* spp. cannot repair damage or reattach but torn fronds could still photosynthesise and produce gametes. Tearing and cutting of the fronds have been shown to stimulate gamete production and damaged plants would still be able to grow and reproduce.

Soft bodied species such as anemones are likely to be damaged or removed by abrasion, although anemones may repair damage and fragments may regrow. The barnacles, limpets and littorinids that occur in this biotope, have some protection from hard shells or plates but abrasion may damage and kill individuals or detach these. All removed barnacles would be expected to die as there is no mechanism for these to reattach. Removal of limpets and barnacles may result in these being displaced to a less favourable habitat and injuries to foot muscles in limpets may prevent reattachment. Although limpets and littorinids may be able to repair shell damage, broken shells while healing will expose the individual to more risk of desiccation and predation. Evidence for the effects of abrasion is provided by a number of experimental studies on trampling (a source of abrasion) and on abrasion by wave thrown rocks and pebbles.

The effects of trampling on barnacles appear to be variable with some studies not detecting significant differences between trampled and controlled areas (Tyler-Walters & Arnold, 2008). However, this variability may be related to differences in trampling intensities and abundance of populations studied. The worst case incidence was reported by Brosnan & Crumrine (1994) who found that a trampling pressure of 250 steps in a 20x20 cm plot one day a month for a period of a year significantly reduced barnacle cover (*Semibalanus glandula* and *Chthamalus dalli*) at two study sites. Barnacle cover reduced from 66% to 7% cover in 4 months at one site and from 21% to 5% within 6 months at the second site. Overall barnacles were crushed and removed by trampling. Barnacle cover remained low until recruitment the following spring. Long *et al.* (2011) also found that heavy trampling (70 humans /km/hr) led to reductions in barnacle cover. Single step experiments provide a clearer, quantitative indication of sensitivity to single events of direct abrasion. Povey & Keough (1991) in experiments on shores in Mornington peninsula, Victoria, Australia, found that in single step experiments 10 out of 67 barnacles, (*Chthamalus antennatus* about 3 mm long), were crushed. However, on the same shore, the authors found that limpets may be relatively more resistant to abrasion from trampling. Following step and kicking experiments, few individuals of the limpet *Cellana trasomerica*, (similar size to *Patella vulgata*) suffered damage or relocated (Povey & Keough, 1991). One kicked limpet (out of 80) was broken and 2 (out of 80) limpets that were stepped on could not be relocated the following day (Povey & Keough, 1991). On the same shore, less than 5% of littorinids were crushed in single step experiments (Povey & Keough, 1991).

Shanks & Wright (1986), found that even small pebbles (<6 cm) that were thrown by wave action in Southern California shores could create patches in aggregations of the barnacle, *Chthamalus fissus*, and could smash owl limpets (*Lottia gigantea*). Average, estimated survivorship of limpets at a wave exposed site, with many loose cobbles and pebbles allowing greater levels of abrasion was 40% lower than at a sheltered site. Severe storms were observed to lead to the almost total destruction of local populations of limpets through abrasion by large rocks and boulders. In sites with mobile cobbles and boulders increased scour results in lower densities of *Littorina* spp. compared with other, local sites with stable substratum (Carlson *et al.*, 2006).

Sensitivity assessment Based on the available evidence it is concluded that the biotope is sensitive to abrasion and that resistance of characterizing and associated species (excluding *Corallina officinalis*) is 'Low' (loss of 25-75% of bed within direct impact footprint), resilience is assessed as 'Medium' (based on *Mytilus edulis*), resulting in a sensitivity of 'Medium'.

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)

High

Q: High A: Medium C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: Medium

Intertidal biotopes will only be exposed to this pressure when submerged during the tidal cycle and thus have limited exposure. Siltation, which may be associated with increased suspended solids and the subsequent deposition of these is assessed separately (see siltation pressures). In general, increased suspended particles reduce light penetration and increase scour and deposition. They may enhance food supply to filter or deposit feeders (where the particles are organic in origin) or decrease feeding efficiency (where the particles are inorganic and require greater filtration efforts). This biotope is sand or silt affected (Connor *et al.*, 2004) and may, therefore, experience episodes with relatively high levels of turbidity from resuspension, an increase at the pressure benchmark for extended periods may exceed tolerances of sensitive species.

Mytilus edulis does not rely on light penetration for photosynthesis. In addition, visual perception is limited and the species does not rely on sight to locate food or other resources. An indirect effect of increased turbidity and reduced light penetration may be reduced phytoplankton productivity which could reduce the food availability for *Mytilus edulis*. However, as *Mytilus edulis* uses a variety of food sources and food is brought in from other areas with currents and tides, the effect is likely to be minimal. This species and the biotopes it forms are therefore not sensitive to changes in water clarity that refer to light penetration. Some siltation may occur within this biotope (Connor *et al.*, 2004) suggesting that the biotope may experience high levels of suspended sediment from resuspension.

Mytilus edulis are often found in areas with high levels of turbidity. For example, the average suspended particulate matter (SPM) concentration at Hastings Shingle Bank was 15 -20 mg/l in June 2005, reaching 50 mg/l in windier (force 4) conditions, although a concentration of 200 mg/l was recorded at this site during gales (Last *et al.*, 2011).

Winter (1972, cited by Moore, 1977) recorded 75 % mortality of *Mytilus edulis* in concentrations of 1.84-7.36 mg/l when food was also available. However, a relatively small increase in SPM concentration e.g. from 10 mg/l to 90 mg/l was found to increase growth rates (Hawkins *et al.*, 1996). Concentrations above 250 mg/l have been shown to impair the growth of filter-feeding organisms (Essink, 1999). But Purchon (1937) found that concentrations of particulates as high as 440 mg/l did not affect *Mytilus edulis* and that mortality only occurred when mud was added to the experiment bringing the concentrations up to 1220 mg/l. The reason for some of the discrepancy between studies may be due to the volume of water used in the experiment. Loosanoff (1962) found that in small quantities of turbid water (due to particulates) the mussel can filter out all of the particulates within a few minutes whereas in volumes >50 gallons per individual the mussel becomes exhausted before the turbidity has been significantly lowered, causing it to close its shell and die.

It may be possible for *Mytilus edulis* to adapt to a permanent increase in SPM by decreasing their gill size and increasing their palp size in areas of high turbidity (Theisen, 1982; Essink, 1999). In areas of variable SPM, it is likely that the gill size would remain the same but the palp would adapt (Essink, 1999). Whilst the ability to adapt may prevent immediate declines in health, the energetic costs of these adaptations may result in reduced fitness; the extent of which is still to be established.

Mytilus edulis uses the circadian clock to determine the opening of the shell gape in nocturnal gape cycles (Ameyaw-Akumfi & Naylor, 1987). Last *et al.* (2011) investigated the effects on increased SPM concentrations on both the gape pattern and mortality in order to establish the effect that aggregate dredging will have on *Mytilus edulis* and other benthic invertebrates. Therefore they tested concentrations similar to those expected within a few hundred meters of an aggregate extraction site. The highest concentration tested using a pVORT (paddle VOrtex Resuspension Tanks) was ~71 mg/l. They showed that there is a significant reduction of the strength of the nocturnal gape cycle at high suspended sediment loads as well as a change in the gape period. The effects of these changes are not fully known but as it is likely that the gape pattern is a strategy to avoid diurnal predators the change may result in an increased risk of predation. After continued measurements of the gape cycle for 4 days post treatment, Last *et al.*, (2011) observed that the cycle took longer than this to recover from the cycle disruption. Further study is required to determine the length of time required for recovery of this behavioural response (Last *et al.*, 2011).

Based on a comprehensive literature review, Moore (1977) concluded that *Mytilus edulis* displayed a higher tolerance to high SPM concentrations than many other bivalves although the upper limit of this tolerance was not certain. He also hypothesised that the ability of the mussel to clean its shell in such conditions played a vital role in its success along with its pseudofaecal expulsion.

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

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

Increases in the cover of sediment trapping, turf forming algae at the expense of canopy forming species have been observed worldwide in temperate systems and have been linked to increased suspended solids linked to human activities worldwide (Airoldi, 2003). *Corallina* species accumulate more sediment than any other alga (Hicks, 1985). Hence an increase in suspended sediment is likely to accumulate in the patches of *Corallina officinalis*. A significant increase may result in smothering (see siltation pressures). An accumulation of sediment within the turf may attract more sediment dwelling interstitial invertebrates such as nematodes, harpacticoids and

polychaetes, although in more wave exposed locations accumulation of sediment is likely to be minimal. Increased suspended sediment may also result in increased scour, which may adversely affect *Fucus vesiculosus* and foliose red algae, and interfere with settling spores and recruitment if the factor is coincident with their major reproductive period. However, coralline algae, especially the crustose forms are thought to be resistant of sediment scour (Littler & Kauker, 1984), and will probably not be adversely affected at the benchmark level.

This community is unlikely to be dependent on suspended sediment. A reduction in suspended sediment will probably reduce the risk of scour, and reduce food availability (where suspended solids are organic) for *Mytilus edulis* and other suspension feeding species in the biotope, although effects are not likely to be lethal.

Experiments have shown that *Ulva* is a shade tolerant genus and can compensate for reduced irradiance by increasing chlorophyll concentration and light absorption at low light levels. *Ulva* spp. were able to survive over two months in darkness and to begin photosynthesizing immediately when returned to the light (Vermaat & Sand-Jensen, 1987). Limited shading from suspended sediments is therefore not considered to negatively affect this genus.

Sensitivity assessment. The exposure of this biotope to suspended sediments in the water column will be limited to immersion periods, and wave action will reduce accumulation. The biotope is considered to be 'Not sensitive' to a reduction in suspended solids, although this may reduce food supply to *Mytilus edulis*, barnacles and other filter and deposit feeders that occur in this biotope. The available evidence suggests that *Mytilus edulis* is likely to tolerate an increase in suspended sediment at the pressure benchmark (an increase from clear to intermediate on the UK TAG, 2014 scale). An increase in suspended solids may lead to some sub-lethal abrasion of fronds of *Fucus vesiculosus* and some reduction in photosynthesis while submerged. Evidence globally indicates that increased suspended solids favour the turf-forming algae that occur within this biotope (Airoldi, 2003). Resistance is therefore assessed as 'Low-Medium' and resilience as 'High' so that sensitivity of the biotope is considered to be 'Low'. An increase in suspended solids above the pressure benchmark may result in a change in species composition with an increase in species seen in very turbid, silty environments e.g. *Ahnfeltia plicata*, *Rhodothamniella floridula*, *Polyides rotunda* and *Furcellaria lumbricalis*.

Smothering and siltation rate changes (light)

Medium

Q: High A: High C: Medium

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Medium C: Medium

Sedimentation can directly affect assemblages inhabiting rocky shores in different ways, particularly by the burial/smothering and scour or abrasion of organisms. This biotope occurs in moderately exposed to exposed conditions. In areas with greater water flow or wave action, excess sediments will be removed from the rock surface within a few tidal cycles, reducing the time of exposure to this pressure. This biotope is described as silted (Connor *et al.*, 2004) and the species composition and abundances may already reflect periodic burial, suggesting that the biotope may not undergo dramatic changes following a siltation event at the pressure benchmark.

Mytilus edulis occur in areas of high suspended particulate matter (SPM) and therefore a level of siltation is expected from the settling of SPM. In addition, the high rate of faecal and pseudofaecal matter production by the mussels naturally results in siltation of the seabed, often resulting in the formation of large mounds beneath the mussel bed. For example, at Morecambe Bay, an accumulation of mussel mud (faeces, pseudofaeces and washed sand) of 0.4-0.5 m between May 1968 and September 1971 resulted in the mortality of young mussels (Daly & Mathieson, 1977).

In order to survive the mussels needed to keep moving upwards to stay on the surface. Many individuals did not make it to the surface and were smothered by the accumulation of mussel mud (Daly & Mathieson, 1977) so that whilst *Mytilus edulis* does have the capacity to vertically migrate through sediment some individuals will not survive.

Sand burial has been shown to determine the lower limit of *Mytilus edulis* beds (Daly & Mathieson, 1977). Burial of *Mytilus edulis* beds by large-scale movements of sand and resultant mortalities have been reported from Morecambe Bay, the Cumbrian coast and Solway Firth (Holt *et al.*, 1998). Essink (1999) recorded fatal burial depths of 1-2 cm for *Mytilus edulis* and suggested that they had a low tolerance of sedimentation based on investigations by R.Bijkerk (cited by Essink, 1999). Essink (1999) suggested that deposition of sediment (mud or sand) on shallow mussel beds should be avoided. However, Widdows *et al.* (2002) noted that mussels buried by 6 cm of sandy sediment (caused by resuspension of sediment due to turbulent flow across the bed) were able to move to the surface within one day. Conversely, Condie (2009) (cited by Last *et al.*, 2011) reported that *Mytilus edulis* was tolerant of repeated burial events.

Last *et al.* (2011) carried out burial experiments on *Mytilus edulis* in pVORTs. They used a range of burial depths and sediment fractions and temperatures. It was found that individual mussels were able to survive burial in depths of 2, 5 and 7 cm for over 32 days although the deeper and longer the mussels were buried the higher the mortality. Only 16% of buried mussels died after 16 days compared to almost 50% mortality at 32 days. Mortality also increased sharply with a decrease in particle size and with increases in temperature from 8.0 and 14.5 to 20 °C. The ability of a proportion of individuals to emerge from burial was again demonstrated with approximately one quarter of the individuals buried at 2 cm resurfacing. However, at depths of 5 cm and 7 cm no emergence was recorded (Last *et al.*, 2011). The lower mortality when buried in coarse sands may be related to the greater number of individuals who were able to emerge in these conditions and emergence was to be significant for survival.

It is unclear whether the same results would be recorded when mussels are joined by byssal threads or whether this would have an impact on survival (Last *et al.*, 2011), although Daly & Mathieson (1977) recorded loose attachments between juvenile mussels during a burial event and some of these were able to surface. It was not clear whether the same ability would be shown by adult mussels in a more densely packed bed.

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

In general, propagules, early post-settlement stages and juveniles suffer severe stress and mortality from sediments (Devinny & Vorse, 1978; Eriksson & Johansson, 2003; Berger *et al.* 2003; Vadas *et al.*, 1992; Airoldi, 2003). Moss *et al.*, (1973), for example, found that growth of zygotes of *Himantalia elongata* was inhibited by a layer of silt 1-2 mm thick and that attachment on silt was insecure.

Increased abundance of algal turfs worldwide has been linked to sediment perturbations although not all the pathways and mechanisms of these effects are clear (see review by Airoidi, 2003). However, even the most tolerant of organisms would eventually suffer from inhibition and mortality following smothering although the thresholds for these effects have not been identified (Airoidi, 2003). *Corallina officinalis* and others within the genus (e.g. *Corallina pinnatifolia* and *Corallina vancouveriensis*) are found on shores subject to high rates of sedimentation that are periodically disturbed by sand burial and scour (Stewart, 1989). Coralline turfs also trap sediments within the turf. The amount of sediment present and the associated fauna varies naturally depending on local conditions such as wave exposure (Dommasnes, 1969). On intertidal shores in southern California the amount of sediment trapped within turfs of *Corallina* spp. varied seasonally from <5 mm to >4.5 cm and was closely related to species composition and the structure of the turf. Airoidi (2003) identified a number of morphological, physiological and life history traits that conferred high levels of tolerance to sedimentation. Those shared by *Corallina* spp are the regeneration of upright fronds from a perennial basal crust resistant to burial and scour, calcified thalli, apical meristems, large reproductive outputs, lateral vegetative growth and slow growth rates (Airoidi, 2003). Experimental deposition of sand on coralline turfs and maintained at 3 cm or 6 cm for one month via daily top-ups did not remove the turfs but did lead to rapid (within 1 hours changes in the invertebrate species as highly mobile species moved away from the turf with later colonisation by sand adapted species (Huff & Jarett, 2007). The community had recovered one month after sand deposition ceased (Huff & Jarett, 2007).

Observations and experiments indicate that *Ulva* spp. have relatively high tolerances for the stresses induced by burial such as darkness, hypoxia and exposure to sulphides (Vermaat & Sand-Jensen, 1987; Corradi et al., 2006; Kamermans et al., 1998). *Ulva lactuca* is a dominant species on sand-affected rocky shores in New Hampshire (Daly & Mathieson, 1977) although Littler et al., (1983) suggest that *Ulva* sp., are present in areas periodically subject to sand deposition not because they are able to withstand burial but because they are able to rapidly colonise sand-scoured areas. *Ulva* spp. have, however, been reported to form turfs that trap sediments (Airoidi, 2003, references therein) suggesting that resistance to chronic rather than acute siltation events may be higher.

The associated species, *Patella vulgata* and *Littorina* spp. are likely to be negatively affected by siltation (Airoidi & Hawkins, 2007; Chandrasekara & Frid, 1998; Albrecht & Reise 1994). Experiments have shown that the addition of even thin layers of sediment (approximately 4 mm) inhibit grazing and result in loss of attachment and death after a few days (Airoidi & Hawkins, 2007). The laboratory experiments are supported by observations on exposed and sheltered shores with patches of sediment around Plymouth in the south west of England as *Patella vulgata* abundances were higher where deposits were absent (Airoidi & Hawkins (2007). Littler et al. (1983) found that the another limpet species, *Lottia gigantea* on southern Californian shores was restricted to refuges from sand burial on shores subject to periodic inundation by sands.

Sensitivity assessment. Deposition of 5 cm of fine material (see benchmark) in a single incident is unlikely to result in significant mortality in blue mussel beds before sediments are removed by current and wave action. However, the inability of *Mytilus edulis* to emerge from sediment deeper than 2 cm (Last et al., 2011, Essink, 1999, Daly & Matthieson, 1977) and the increased mussel mortality with depth and reduced particle size observed by Last et al. (2011) suggest that there may be some mortality and resistance is assessed as 'Medium'. Survival will be higher in winter months when temperatures are lower and physiological demands are decreased. Burial will lower survival and germination rates of spores and cause some mortality in early life stages of *Fucus*

vesiculosus and foliose red algae. Adults are more resistant but will experience a decrease in growth and photosynthetic rates. Mortality will be more limited and possibly avoided, where the smothering sediment is removed due to wave action or tidal streams, depending on how long the sediment remains. Resistance and resilience have both been assessed as 'Medium' based on *Mytilus edulis* and macroalgae. Overall the biotope has a 'Medium' sensitivity to smothering at the level of the benchmark. It should be noted that the associated *Patella vulgata* and littorinids may have higher sensitivities to this pressure.

Smothering and siltation rate changes (heavy)

Medium

Q: Low A: NR C: NR

Medium

Q: High A: Low C: Medium

Medium

Q: Low A: Low C: Low

Sensitivity to this pressure will be mediated by site-specific hydrodynamic conditions and the footprint of the impact. Where a large area is covered sediments may be shifted by wave and tides rather than removed. However, mortality will depend on the duration of smothering, where wave action rapidly mobilises and removes fine sediments, survival may be much greater. No evidence was found to assess this pressure at the benchmark. A deposit at the pressure benchmark would cover all species with a thick layer of fine materials. Species associated with this biotope such as limpets and littorinids would not be able to escape and would likely suffer mortality (see evidence for light siltation).

Mytilus edulis may be able to survive if the deposit was rapidly removed and the depth decreased. Last *et al.*, (2011) carried out burial experiments on *Mytilus edulis* in pVORTs. They used a range of burial depths and sediment fractions and temperatures. It was found that individual mussels were able to survive burial in depths of 2, 5 and 7 cm for over 32 days although the deeper and longer the mussels were buried the higher the mortality. Only 16 % of buried mussels died after 16 days compared to almost 50 % mortality at 32 days. Mortality also increased sharply with a decrease in particle size and with increases in temperature from 8.0 and 14.5 to 20 °C. Several studies found that increasing the vertical sediment burden negatively impact fucoids survival and associated communities. Even the most tolerant of organisms would eventually suffer from inhibition and mortality following smothering although the thresholds for these effects have not been identified (Airoldi, 2003).

Sensitivity assessment. At the level of the benchmark (30 cm of fine material added to the seabed in a single event) smothering is likely to result in mortalities of *Mytilus edulis* understorey algae, invertebrate grazers and young (germling) fucoids. Resistance is assessed as 'Low' as all individuals exposed to siltation at the benchmark level are predicted to die and a 'Medium' resilience. Overall the biotope has a 'Medium' sensitivity to siltation at the pressure benchmark.

Litter

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed.

Electromagnetic changes

No evidence (NEv)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

No evidence.

Underwater noise changes

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant.

Introduction of light or shading

High

Q: Low A: NR C: NR

High

Q: High A: High C: High

Not sensitive

Q: Low A: Low C: Low

Increased levels of diffuse irradiation correlate with increased growth in macroalgae (Aguilera *et al.*, 1999). Levels of diffuse irradiation increase in summer, and with a decrease in latitude. As *Fucus vesiculosus* is found in the middle its natural range in the British Isles an increase in the level of diffuse irradiation will not cause a negative impact on the species or the biotope. However, it is not clear how these findings may reflect changes in light levels from artificial sources, and whether observable changes would occur at the population level as a result.

Corallina officinalis are shade tolerant algae, often occurring under a macroalgal canopy that reduces light penetration. In areas of higher light levels, the fronds may be lighter in colour due to bleaching (Colhart & Johansen, 1973). Other red algae in the biotope are flexible with regard to light levels.

Canopy removal experiments in a rocky sub tidal habitat in Nova Scotia, Canada by Schmidt & Scheibling (2007) did not find a shift in understory macroalgal turfs (dominated by *Corallina officinalis*, *Chondrus crispus* and *Mastocarpus stellatus*) to more light-adapted species over 18 months. *Corallina officinalis* may be overgrown by epiphytes, especially during summer.

Sensitivity assessment. As the key structuring and characterizing species colonize a broad range of light environments and shaded understory habitats the biotope is considered to have 'High' resistance and, by default, 'High' resilience and therefore is 'Not sensitive' to this pressure.

Barrier to species movement

High

Q: Low A: NR C: NR

High

Q: High A: High C: High

Not sensitive

Q: Low A: Low C: Low

No direct evidence was found to assess this pressure. As the larvae of *Mytilus edulis* are planktonic and are transported by water movements, barriers that reduce the degree of tidal excursion may alter the supply of *Mytilus edulis* to suitable habitats from source populations. However, the presence of barriers may enhance local population supply by preventing the loss of larvae from enclosed habitats. This species is therefore potentially sensitive to barriers that restrict water movements, whether this will lead to beneficial or negative effects will depend on whether enclosed populations are sources of larvae or are 'sink' populations that depend on outside supply of larvae to sustain the local population. The associated macroalgae (with the exception of *Ulva* spp.) have limited dispersal. Barriers and changes in tidal excursion are not considered relevant to these species as dispersal is limited. As the key characterizing species *Mytilus edulis* are widely distributed and have larvae capable of long distance transport, resistance to this pressure is assessed as 'High' and resilience as 'High' by default. This biotope is therefore considered to be 'Not sensitive'.

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

Not relevant.

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	No evidence (NEv)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Within this biotope this pressure is only relevant to *Mytilus edulis* as other species present are not cultivated or translocated. Commercial cultivation of *Mytilus edulis* involves the collection of juvenile mussel 'seed' or spat (newly settled juveniles ca 1-2 cm in length) from wild populations, with subsequent transportation around the UK for re-laying in suitable habitats. As the seed is harvested from wild populations from various locations the gene pool will not necessarily be decreased by translocations. Movement of mussel seed has the potential to transport pathogens and non-native species (see relevant pressure sections). This pressure assessment is based on Mainwaring *et al.* (2014) and considers the potential impacts on natural mussel beds of genetic flow between translocated stocks and wild mussel beds.

Commercial cultivation of *Mytilus edulis* involves the collection of juvenile mussel 'seed' or spat (newly settled juveniles ca 1-2 cm in length) from wild populations, with subsequent transportation around the UK for re-laying in suitable habitats. As the seed is harvested from wild populations from various locations the gene pool will not necessarily be decreased by translocations. Movement of mussel seed has the potential to transport pathogens and non-native species (see relevant pressure sections). This pressure assessment is based on Mainwaring *et al.* (2014) and considers the potential impacts on natural mussel beds of genetic flow between translocated stocks and wild mussel beds.

Two species of *Mytilus* occur in the UK, *Mytilus edulis* and *Mytilus galloprovincialis*. *Mytilus edulis* appears to maintain genetic homogeneity throughout its range whereas *Mytilus galloprovincialis* can be genetically subdivided into a Mediterranean group and an Atlantic group (Beaumont *et al.* 2007). *Mytilus edulis* and *Mytilus galloprovincialis* have the ability to hybridise in areas where their distribution overlaps e.g. around the Atlantic and European coast (Gardner, 1996; Daguin *et al.*, 2001; Bierne *et al.*, 2002; Beaumont *et al.*, 2004). In the UK overlaps occur on the North East coast, North East Scotland, South West England and in the North, West and South of Ireland (Beaumont *et al.*, 2007). It is difficult to distinguish *Mytilus edulis*, *Mytilus galloprovincialis* or hybrids based on shell shape because of the extreme plasticity of shape exhibited by mussels under environmental variation, and a genetic test is required (Beaumont *et al.*, 2007). There is some discussion questioning the distinction between the two species as the hybrids are fertile (Beaumont *et al.*, 2007). Hybrids reproduce and spawn at a similar time to both *Mytilus edulis* and *Mytilus galloprovincialis* which supports genetic flow between the taxa (Doherty *et al.*, 2009).

There is some evidence that hybrid larvae have a faster growth rate to metamorphosis than pure individuals which may leave pure individuals more vulnerable to predation (Beaumont *et al.*, 1993). As the physiology of both the hybrid and pure *Mytilus edulis* is so similar there is likely to be very little impact on the tolerance of the bed to neither pressures nor a change in the associated fauna.

A review by Svåsand *et al.* (2007) concluded that there was a lack of evidence distinguishing between different populations to accurately assess the impacts of hybridisation and in particular how the gene flow may be affected by aquaculture. Therefore, it cannot be confirmed whether farming will have an impact on the genetics of this species beyond a potential for increased hybridisation.

The key characterizing species *Fucus vesiculosus* is not currently cultivated or translocated. Pressures that alter the genetic diversity of populations may lead to negative impacts. Genetically diverse populations are generally more resilient to changes in environmental conditions compared to genetically conserved populations. Tatarenkov *et al.* (2007) determined a high level of genetic variation in *Fucus vesiculosus* and extensive phenotypic variation. They suggested this might explain why the species is more successful than most furoid species in colonizing marginal marine environments such as low-salinity estuaries, showing a range of morphological, physiological and ecological adaptations (Tatarenkov *et al.* 2005). Pressures causing a rapid change will have a greater impact as the natural ability of the species to adapt is compromised.

No information was found on current production of *Mastocarpus stellatus*, *Chondrus crispus* or other turf forming red seaweeds in the UK and it is understood that wild harvesting rather than cultivation is the method of production. No evidence was found for the effects of gene flow between cultivated species and wild populations. *Palmaria palmata* may be cultivated for use as biofilters and/or food. Experiments by van der Meer (1987) found that the hybrids of *Palmaria palmata* crosses from Canada and Ireland had vigorous growth and normal morphology, however the tetraspores had lower viability and those that germinated produced abnormal sporelings. It was concluded that populations from Ireland and Canada represent the same species that is in the process of splitting into sibling species. Populations around the UK express different haplotypes (Provan *et al.*, 2005) indicating some genetic variation between populations. Although cultivation of different genotypes may lead to gene flow between wild and cultivated populations the limited dispersal may reduce exposure. Some negative effects may arise from hybridisation between very geographically separated populations but there is no evidence to suggest that gene flow between different UK haplotypes would lead to negative effects. Although cultivation of different genotypes may lead to gene flow between wild and cultivated populations the limited dispersal may reduce exposure.

Sensitivity assessment. No direct evidence was found regarding the potential for negative impacts of translocated mussel seed on adjacent natural beds. While it is possible that translocation of mussel seed could lead to genetic flow between cultivated beds and local wild populations, there is currently no evidence to assess the impact (Svåsand *et al.*, 2007). Hybrid beds perform the same ecological functions as *Mytilus edulis* so that any impact relates to genetic integrity of a bed alone. This impact is considered to apply to all mussel bed biotopes equally, as the main habitat forming species *Mytilus edulis* is translocated. Also, given the uncertainty in identification of the species, habitats or biotopes described as dominated by *Mytilus edulis* may well be dominated by *Mytilus galloprovincialis*, their hybrids or a mosaic of the three. Presently, there is no evidence of impact due to genetic modification and translocation; therefore 'No evidence' is reported. The range of *Mytilus galloprovincialis* is thought to be extending northwards (Beaumont *et al.*, 2007) and this assessment may require updating in the future. The pressure is considered to be 'Not relevant' to

other species within the biotope.

Introduction or spread of invasive non-indigenous species

Low

Q: High A: Medium C: High

Very Low

Q: High A: Low C: Medium

High

Q: High A: Low C: Medium

Invasive non-indigenous species (INIS) that can alter habitats (ecological engineers), or out-compete *Mytilus edulis* and the native macroalgae for space and other resources such as light and nutrients, are the most likely species to negatively affect this biotope. Space pre-emption by *Mytilus edulis*, *Fucus vesiculosus* and the turf and crustose bases of the red macroalgae, as well as the trapped sediment within the turf, may prevent settlement of INIS until disturbance events create gaps for invasion. However, in the Mediterranean crustose corallines and algal turfs facilitate attachment of *Caulerpa racemosa* by providing a more complex substratum than bare rock (Bulleri & Benedetti-Cecchi, 2008).

Algal species which may have overlapping habitat requirements include the green seaweed *Codium fragile* subsp *tormentosoides* (now renamed as *Codium fragile fragile*) and the red seaweed *Heterosiphonia japonica*, neither of these have so far been recorded in nuisance densities (Sweet, 2011j). Wireweed, *Sargassum muticum*, grows best on sheltered shores and in rockpools (Sewell, 2011c), rather than the exposed shores characteristic of this biotope. The red seaweeds *Heterosiphonia japonica* and *Neosiphonia harveyi* may also occur in this biotope but again no impacts have been reported. The tunicates *Didemnum vexillum* and *Asterocarpa humilis*, the hydroid *Schizoporella japonica* and the bryozoan *Watersipora subatra* (Bishop, 2012c, Bishop, 2015a and b; Wood, 2015) are currently only recorded from artificial hard substratum in the UK and it is not clear what their established range and impacts in the UK would be.

A significant potential INIS is the Pacific oyster *Magallana gigas*, as its distribution and environmental tolerances are considered to overlap with this biotope and this reef forming species can alter habitat structure. This species may also affect the grazers present in the biotope. In the Wadden Sea and North Sea, *Magallana gigas* overgrows mussel beds in the intertidal zone (Diederich, 2005, 2006; Kochmann *et al.*, 2008), although larvae did show preference for settling on conspecifics before the mussels and struggled to settle on mussels with a fucoid covering. It has been observed that mussel beds in the Wadden Sea that are adjacent to oyster farms were quickly converted to oyster beds (Kochmann *et al.*, 2008). Padilla (2010) predicted that *Magallana gigas* could either displace or overgrown mussels on rocky and sedimentary habitats of low or high energy

Magallana gigas is the most widely grown bivalve in aquaculture around the world at present and an important nuisance species in marine waters (Padilla, 2010). Adults are also long-lived so that populations can survive with infrequent recruitment. It has a high fecundity, a long-lived pelagic larval phase and hence high dispersal potential (>1000km). *Magallana gigas* does not spawn at water temperatures below ca 20°C but adults grow in colder waters, so that it was thought that this species could not escape from cultivation in cold water areas. However, it has been suggested that climate change and warmer waters have allowed *Magallana gigas* to expand into and reproduce in previously unsuitable areas. Established feral populations have been reported to spread via larvae (Padilla, 2010). It is found from the mid-littoral to the upper subtidal, and grows on hard substrata but also on other bivalves (e.g. blue mussels) and polychaete reefs (Padilla, 2010).

Diederich (2005, 2006) examined settlement, recruitment and growth of *Magallana gigas* (as

Crassostrea gigas) and *Mytilus edulis* in the northern Wadden Sea. *Magallana gigas* recruitment success was dependant on temperature, and in the northern Wadden Sea, only occurred in six of the 18 years since *Magallana gigas* was first introduced. Survival of juveniles is higher in mild than cold winters. Also survival of both juveniles and adults on mussel beds is higher than that of the mussels themselves. However, recruitment of *Magallana gigas* was significantly higher in the intertidal than the shallow subtidal, although the survival of adult oysters or mussels in the subtidal is limited by predation. Diederich (2005) concluded that hot summers could favour *Magallana gigas* reproduction while cold winters could lead to high mussel recruitment the following summer. Diederich (2005, 2006) noted that the high survival rate of *Magallana gigas* adults and juveniles in the intertidal was likely to compensate for years of poor recruitment. *Magallana gigas* also prefer to settle on conspecifics, so that it can build massive oyster reefs, which themselves are more resistant to storms or ice scour than the mussel beds they replace; as oysters are cemented together, rather than dependent on byssus threads. *Magallana gigas* also grows faster than *Mytilus edulis* in the intertidal and reaches by ca 2-3 times the length of mussels within one year. In addition, growth rates in *Magallana gigas* were independent of tidal level (emergence regime, substratum, *Fucus* cover and barnacle epifauna (growing on both mussels and oysters), while growth rate of *Mytilus edulis* was decreased by these factors. The faster growth rate could make *Magallana gigas* more competitive than *Mytilus edulis* where space or food is limiting. Diederich (2006) concluded that the massive increase in *Magallana gigas* in the northern Wadden Sea was caused by high recruitment success, itself due to anomalously warm summer temperatures, the preference for settlement on conspecifics (and hence reef formation), and high survival rates of juveniles. As oyster reefs form on former mussel beds, the available habitat for *Mytilus edulis* could be restricted (Diederich, 2006).

Dense aggregations of *Magallana gigas* on a former mussel bed showed increased abundance and biomass of *Littorina littorea* in the Wadden Sea (Markert *et al.* 2010). However, Eschweiler & Buschbaum (2011) found that juvenile *Littorina littorea* could carry *Magallana gigas* and *Crepidula fornicata* as epibionts. Body dry weight of snails without oyster overgrowth was twice as high compared to winkles covered with oysters. Also crawling speed of snails with oyster epigrowth was significantly slowed down and about ten times lower than in unfouled periwinkles. Additionally, oyster epibionts caused a strong decrease in reproductive output. In laboratory experiments, egg production of fouled *Littorina littorea* was about 100-fold lower than in affected individuals. Field surveys in different years and habitats demonstrated that up to 10% of individuals occurring on epibenthic bivalve beds and up to 25% of snails living on sand flats may be fouled by *Magallana gigas*.

Thompson & Schiel (2012) found that native fucoids show high resistance to invasions by the Japanese kelp *Undaria pinnatifida*. However cover of *Fucus vesiculosus* was inversely correlated with the cover of the invasive *Sargassum muticum* indicating competitive interaction between the two species (Stæhr *et al.*, 2000). Stæhr *et al.* (2000) determined that the invasion of *Sargassum muticum* could affect local algal communities through competition mainly for light and space. Hammann *et al.*, (2013) found that in the Baltic Sea *Gracilaria vermiculophylla* could impact *Fucus vesiculosus* through direct competition for resources, decreasing the half-life of germlings, and increasing the level of grazing pressure. To date *Gracilaria vermiculophylla* has only been recorded in Northern Ireland, and not on mainland Britain. The introduction of this species to intertidal rocky shores around the British Isles could have negative impacts on native fucoids, and could become relevant to this specific biotope.

The non-native crab *Hemigrapsus sanguineus* has recently been recorded in the UK (Sweet & Sewell, 2014) and has the potential to be a significant predator of intertidal invertebrates. Significant

reductions in common shore crab abundance and mussel density have been reported where the crab has achieved high densities in mainland Europe (Sweet & Sewell, 2014). Mortalities of 25% of juvenile *Mytilus edulis* were attributed to predation by *Hemigrapsus sanguineus* in an intertidal habitat of western Long Island Sound along the Connecticut coastline (Brousseau *et al.*, 2014). In Rye, New York, declines of approximately 80% of *Littorina littorea* in the intertidal were reported to coincide with an expansion of the *Hemigrapsus sanguineus* population (Kraemer *et al.*, 2007). This crab occurs on exposed shores and may therefore occur in this biotope when established. If predation of littorinids was significantly increased this could impact the algal composition and abundance of this biotope by altering the level of grazing pressure.

Sensitivity assessment. Little evidence was found to assess the impact of INIS on this biotope and much of the evidence comes from intertidal habitats in other countries. The conversion of this biotope to a *Magallana gigas* reef would represent a significantly negative impact. Replacement of red algal turfs by other similar species may lead to some subtle effects on local ecology but at low abundances the biotope would still be recognisable from the description. Based on *Magallana gigas* biotope resistance to this pressure is assessed as 'Low'. The biotope will only recover if these species are removed, either through active management or natural processes. To recognise that recovery may be prolonged, resilience is assessed as 'Very low' and sensitivity is therefore assessed as 'High'.

Introduction of microbial pathogens

Medium
Q: High A: Medium C: Medium

Medium
Q: High A: Low C: Medium

Medium
Q: High A: Low C: Medium

Evidence for the impacts of microbial pathogens on *Mytilus edulis* was reviewed by Mainwaring *et al.* (2014) with specific reference to the shellfish pathogens *Marteilosis* and *Bonamia*. Natural *Mytilus edulis* beds are host to a diverse array of disease organisms, parasites and commensals from many animal and plant groups including bacteria, blue green algae, green algae, protozoa, boring sponges, boring polychaetes, boring lichen, the intermediary life stages of several trematodes, copepods and decapods (Bower, 1992; Gray *et al.*, 1999; Bower, 2010).

Whilst *Bonamia*, has been shown not to infect *Mytilus edulis* (Culloty *et al.*, 1999), *Marteilia refringens* can infect and have significant impacts on the health of *Mytilus edulis*. Its distribution, impacts on the host, diagnostic techniques and control measures are reviewed by Bower (2011). There is some debate as to whether there are two species of *Marteilia*, one which infects oysters (*Marteilia refringens*) and another that infects blue mussels (*Marteilia maurini*) (Le Roux *et al.*, 2001) or whether they are just two strains of the same species (Lopez-Flores *et al.*, 2004; Balseiro *et al.*, 2007). Both species are present in southern parts of the United Kingdom. The infection of *Marteilia* results in *Marteiliosis* which disrupts the digestive glands of *Mytilus edulis* especially at times of spore release. Heavy infection can result in a reduced uptake of food, reduced absorption efficiency, lower carbohydrate levels in the haemolymph and inhibited gonad development particularly after the spring spawning resulting in an overall reduced condition of the individual (Robledo *et al.*, 1995).

Recent evidence suggests that *Marteilia* is transferred to and from *Mytilus edulis* via the copepod *Paracartia grani*. This copepod is not currently prevalent in the UK waters, with only a few records in the English Channel and along the South coast. However, it is thought to be transferred

by ballast water and so localised introductions of this vector may be possible in areas of mussel seed transfer e.g. the Menai Strait. The mussel populations here are considered to be naive (i.e. not previously exposed) and therefore could be heavily affected, although the likelihood is slim due to the dependence on the introduction of a vector that is carrying *Marteilia* and then it being transferred to the mussels.

Berthe *et al.* (2004) concluded that *Mytilus edulis* is rarely significantly affected by *Marteilia* sp. However, occasions have been recorded of nearly 100 % mortality when British spat have been transferred from a 'disease free area' to areas in France where *Marteilia* sp. are present. This suggests that there is a severe potential risk if naive spat are moved around the UK from northern waters into southern waters where the disease is resident (enzootic) or if increased temperatures allow the spread of *Marteilia* sp. northwards towards the naive northern populations. In addition, rising temperatures could allow increased densities of the *Marteilia* sp. resulting in heavier infections which can lead to mortality.

Very little is known about infections in *Fucus* (Wahl *et al.*, 2011). Coles (1958) identified parasitic nematodes that caused galls on *Fucus serratus* in the Southwest of Britain. But to date no mortalities have been associated to the introduction of microbial pathogens. Torchin *et al.* (2002) suggests that there is potential for increased biotic interactions with parasites or pathogens in many marine systems.

Several coralline and non-coralline species are epiphytic on *Corallina officinalis*. Irvine & Chamberlain (1994) cite tissue destruction caused by *Titanoderma corallinae*. However, no information on pathogenic organisms in the UK was found. *Corallina officinalis*, like many other algal species has been demonstrated to produce antibacterial substances (Taskin *et al.*, 2007). No evidence was found for pathogens of the other red algae which may be present in this biotope. The fungal pathogen, *Petersenia palmaria* n. sp (Oomycetes) which infects *Palmaria mollis*, does not affect *Palmaria palmata* (Meer & Poeschel, 1985). Other species associated with this biotope such as littorinids, patellid limpets and barnacles experience low levels of infestation by pathogens but mass-mortalities have not been recorded. For example, parasitism by trematodes may cause sterility in *Littorina littorea*. *Littorina littorea* are also parasitized by the boring polychaete, *Polydora ciliata* and *Cliona* sp, which weakens the shell and increases crab predation. *Semibalanus balanoides* are considered to be subject to persistent, low levels of infection by pathogens and parasites. Barnacles are parasitised by a variety of organisms and, in particular, the cryptoniscid isopod *Hemioniscus balani*, in which heavy infestation can cause castration of the barnacle. At usual levels of infestation these are not considered to lead to high levels of mortality.

Sensitivity assessment. No evidence was found that outbreaks of microbial pathogens significantly impact populations of the key characterizing *Fucus vesiculosus* and other associated algal species. Limpets, barnacles and littorinids may be subject to persistent low levels of infestation by pathogens but these are not recorded to lead to high-levels of mortality. Bower (2010) noted that although *Marteilia* was a potentially lethal pathogen of mussels, most populations were not adversely affected by marteiliosis but that in some areas mortality can be significant in mariculture (Berthe *et al.*, 2004). The resultant population would be more sensitive to other pressures, even where the disease only resulted in reduced condition. Therefore, a precautionary resistance of 'Medium' is suggested (<25% mortality), with a resilience of 'Medium' (2-10 years) resulting in a sensitivity of 'Medium'.

Removal of target species

Low

Q: High A: High C: High

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Direct, physical impacts from harvesting 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 target species on this biotope. Many of the species characterizing or associated with this biotope may be removed by either recreational or commercial harvesters.

Mytilus edulis is a commercially targeted species worldwide and has been fished for hundreds of years and managed in England and Wales for the last hundred years (Holt *et al.*, 1998). Mussels are also regularly hand collected by fisherman for bait and food from intertidal beds which can also result in significant damage to the bed (Holt *et al.*, 1998; Smith & Murray, 2005). Smith & Murray (2005) examined the effects of low level disturbance and removal on an extensive bed of *Mytilus californianus* (composed of a single layer of mussels) in southern California. They observed a significant decrease in mussel mass (g/m^2), density (no/m^2), percentage cover and mean shell length due to low-intensity simulated bait-removal treatments (2 mussels / month) for 12 months (Smith & Murray 2005). They also stated that the initial effects of removal were 'overshadowed' by loss of additional mussels during time periods between treatments, probably due to the indirect effect of weakening of byssal threads attachments between the mussel leaving them more susceptible to wave action (Smith & Murray, 2005). The low-intensity simulated bait-removal treatments had reduced percentage cover by 57.5% at the end of the 12 month experimental period. Smith & Murray (2005) suggested that the losses occurred from collection and trampling are far greater than those that occur by natural causes. This conclusion was reached due to significant results being displayed for human impact despite the experiment taking place during a time of high natural disturbance from El Niño–Southern Oscillation (ENSO). In addition, Holt *et al.*, (1998) recorded an incident of the removal of an entire bed that is adjacent to a road in Anglesey due to fishermen bait collecting. Recreational fishermen will often collect moulting *Carcinus maenas* or whelks by hand from intertidal mussel beds for bait. The removal of predatory crabs could actively benefit *Mytilus edulis*.

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

Stagnol *et al.* (2013) investigated the effects of commercial harvesting of intertidal fucooids on ecosystem biodiversity and functioning. The study found that the removal of the macroalgae canopy affected the metabolic flux of the area. Flows from primary production and community respiration were lower on the impacted area as the removal of the canopy caused changes in temperature and humidity conditions. Suspension feeders were the most affected by the canopy removal as canopy-forming algae are crucial habitats for these species, most of them being sessile organisms. Other studies confirm that loss of canopy had both short and long-term consequences for benthic communities in terms of diversity resulting in shifts in community composition and a loss of ecosystem functioning such as primary productivity (Lilley & Schiel, 2006; Gollety *et al.*, 2008).

Red algae within the biotope may also be subject to hand gathering. *Mastocarpus stellatus* is harvested commercially in Scotland and Ireland to produce carageen, the stipe is removed but the base is left intact to allow the algae to re-grow. *Palmaria palmata* and *Osmundea pinnatifida* are also collected by hand commercially and recreationally for consumption. *Corallina officinalis* is collected for medical purposes; the fronds are dried and converted to hydroxyapatite

and used as bone forming material (Ewers *et al.* 1987). It is also sold as a powder for use in the cosmetic industry.

Littorinids are one of the most commonly harvested species of the rocky shore. Large scale removal of *Littorina littorea* may allow a proliferation of opportunistic green algae, such as *Ulva*, on which it preferentially feeds. Experiments designed to test the effects of harvesting by removing individuals at Strangford Lough found that there was no effect of experimental treatments (either harvesting or simulated disturbance) on *Littorina littorea* abundance or body size over a 12 week period (Crossthwaite *et al.* 2012). This suggests that these animals are generally abundant and highly mobile; thus, animals that were removed were quickly replaced by dispersal from surrounding, un-harvested areas. However, long-term exploitation, as inferred by background levels of harvest intensity, did significantly influence population abundance and age structure (Crossthwaite *et al.* 2012). A broadscale study of harvesting in Ireland using field studies and interviews with wholesalers and pickers did suggest that some areas were over harvested but the lack of background data and quantitative records make this assertion difficult to test (Cummins *et al.*, 2002). Changes in grazer abundance can alter the character of the algal assemblage. Grazer removal (manual removal of all gastropods in pool and a 1m surrounding perimeter) caused strong and highly significant changes in assemblage structure in rockpools that contained red turf forming algae mainly due to an increase in the cover of green filamentous algae and a decrease in cover of live crustose coralline algae (25.40%) (Atalah & Crowe, 2010).

Sensitivity assessment *Mytilus edulis* beds have no avoidance mechanisms to escape targeted harvesting and as a result a significant proportion of the bed can be removed (Palmer *et al.*, 2007; Narvarte *et al.*, 2011). As the majority of the mussel beds that are harvested in the UK are regularly replenished with seed, the recovery rate for maintained beds should be rapid. In natural (wild) beds, the recovery could be significantly longer due to indirect effects from wave action and the sporadic nature of recruitment (Paine & Levin 1981; Seed & Suchanek 1992). Even hand-picking for bait can result in a significant decrease in cover, especially in beds composed of a single layer of mussels (Smith & Murray 2005). It should be noted that dense, multi-layered mussel beds may be more resistant to the gaps and bait collection, as damage to the upper layer may not effect deeper layers, so that attachment to the substratum and each other is maintained (Brosnan & Crumrine, 1994). Based on the available evidence *Mytilus edulis* are considered to have 'Low' resistance to this pressure and 'Medium' resilience so that sensitivity is assessed as 'Medium'. As the other species that are harvested in this biotope are also attached, sedentary or slow moving and relatively conspicuous a single event of targeted harvesting could efficiently remove individuals and resistance is assessed as 'Low'. Resilience of *Fucus vesiculosus*, the turf forming red seaweeds and littorinids is assessed as 'High' (based on evidence for recovery from harvesting that did not damage the algal bases although see caveats in the resilience section) and biotope sensitivity is assessed as 'Low'. This assessment refers to a single collection event, long-term harvesting over wide spatial scales will lead to greater impacts, with lower resistance and longer recovery times. Loss of *Mytilus edulis* would lead to reclassification of the biotope.

Removal of non-target species

Low

Q: Low A: NR C: NR

Medium

Q: High A: Low C: Medium

Medium

Q: Low A: Low C: Low

Direct, physical impacts are assessed through the abrasion and penetration of the seabed pressures, while this pressure considers the ecological or biological effects of by-catch. Removal of a large part of the *Mytilus edulis* bed unintentionally and the loss of the macroalgae would substantially alter the character of the biotope leading to reclassification and alter ecosystem

functions such as rates of production and the provision of a structurally complex habitat.

Sensitivity assessment. The habitat structure created by *Mytilus edulis* is the key characterizing, structural and functional feature of this biotope group. Removal of individuals as by-catch would remove the biotope and hence the biotope is considered to have 'Low' resistance to this pressure and to have 'Medium' resilience (based on *Mytilus edulis*). Sensitivity is therefore 'Medium'.

Bibliography

- Hawkins, S.J., Hartnoll, R.G., Kain, J.M. & Norton, T.A., 1992. *Plant-animal interactions on hard substrata in the North-east Atlantic*, Oxford: Clarendon Press.
- Aguilera, J., Karsten, U., Lippert, H., Voegelé, B., Philipp, E., Hanelt, D. & Wiencke, C., 1999. Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic. *Marine Ecology Progress Series*, **191**, 109-119.
- Airoidi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology: An Annual Review*, **41**, 161-236
- Airoidi, L. & Hawkins, S.J., 2007. Negative effects of sediment deposition on grazing activity and survival of the limpet *Patella vulgata*. *Marine Ecology Progress Series*, **332**, 235-240.
- Akaishi, F.M., St-Jean, S.D., Bishay, F., Clarke, J., Rabbitto, I.d.S. & Ribeiro, C.A., 2007. Immunological responses, histopathological findings and disease resistance of blue mussel (*Mytilus edulis*) exposed to treated and untreated municipal wastewater. *Aquatic Toxicology*, **82** (1), 1-14.
- Albrecht, A. & Reise, K., 1994. Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. *Helgoländer Meeresuntersuchungen*, **48** (2-3), 243-256.
- Alfaro, A.C., 2005. Effect of water flow and oxygen concentration on early settlement of the New Zealand green-lipped mussel, *Perna canaliculus*. *Aquaculture*, **246**, 285-94.
- Alfaro, A.C., 2006. Byssal attachment of juvenile mussels, *Perna canaliculus*, affected by water motion and air bubbles. *Aquaculture*, **255**, 357-61
- Almada-Villela P.C., 1984. The effects of reduced salinity on the shell growth of small *Mytilus edulis* L. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 171-182.
- Almada-Villela, P.C., Davenport, J. & Gruffydd, L.L.D., 1982. The effects of temperature on the shell growth of young *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, **59**, 275-288.
- Alström-Rapaport, C., Leskinen, E. & Pamilo, P., 2010. Seasonal variation in the mode of reproduction of *Ulva intestinalis* in a brackish water environment. *Aquatic Botany*, **93** (4), 244-249.
- Ameyaw-Akumfi, C. & Naylor, E., 1987. Spontaneous and induced components of salinity preference behaviour in *Carcinus maenas*. *Marine Ecology Progress Series*, **37**, 153-158.
- Amsler, C.D. & Searles, R.B., 1980. Vertical distribution of seaweed spores in a water column off shore of North Carolina. *Journal of Phycology*, **16**, 617-619.
- Arnold, D., 1957. The response of the limpet, *Patella vulgata* L., to waters of different salinities. *Journal of the Marine Biological Association of the United Kingdom*, **36** (01), 121-128.
- Atalah, J. & Crowe, T.P., 2010. Combined effects of nutrient enrichment, sedimentation and grazer loss on rock pool assemblages. *Journal of Experimental Marine Biology and Ecology*, **388** (1), 51-57.
- Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Clark, J.A. & Ireland, P.L., 2003. Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biological Conservation*, **114**, 127-141.
- Auker, L.A. & Oviatt, C.A., 2007. Observations on the colonization of the invasive tunicate *Didemnum* sp. in Rhode Island. *In* *Naturalist*, **14**, 1-4.
- Auker, L.A. & Oviatt, C.A., 2008. Factors influencing the recruitment and abundance of *Didemnum* in Narragansett Bay, Rhode Island. *ICES Journal of Marine Science: Journal du Conseil*, **65** (5), 765-769.
- Aunaas, T., Denstad, J-P. & Zachariassen, K., 1988. Ecophysiological importance of the isolation response of hibernating blue mussels (*Mytilus edulis*). *Marine Biology* **98**: 415-9
- Bäck, S., 1993. Morphological variation of northern Baltic *Fucus vesiculosus* along the exposure gradient. *Annales Botanici Fennici*, 275-283.
- Bäck, S., Collins, J. & Russell, G., 1992. Effects of salinity on growth of Baltic and Atlantic *Fucus vesiculosus*. *British Phycological Journal*, **27** (1), 39-47.
- Bahmet, I., Berger, V. & Halaman, V., 2005. Heart rate in the blue mussel *Mytilus edulis* (Bivalvia) under salinity change. *Russian Journal of Marine Biology* **31**: 314-7
- Bailey, J., Parsons, J. & Couturier, C., 1996. Salinity tolerance in the blue mussel, *Mytilus edulis*. *Rep. Report no. 0840-5417*, *Aquaculture Association of Canada*, New Brunswick, Canada
- Baird, R.H., 1966. Factors affecting the growth and condition of mussels (*Mytilus edulis*). *Fishery Investigations. Ministry of Agriculture, Fisheries and Food, Series II*, no. 25, 1-33.
- Ballantine, W., 1961. A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies*, **1**, 73-84.
- Balseiro P., Montes A., Ceschia G., Gestal C., Novoa B. & Figueras A., 2007. Molecular epizootiology of the European Marteilia spp., infecting mussels (*Mytilus galloprovincialis* and *M. edulis*) and oysters (*Ostrea edulis*): an update. *Bulletin of the European Association of Fish Pathologists*, **27**(4), 148-156.
- Bamber, R.N. & Irving, P.W., 1993. The *Corallina* run-offs of Bridgewater Bay. *Porcupine Newsletter*, **5**, 190-197.

- Barnes, H., Finlayson, D.M. & Piatigorsky, J., 1963. The effect of desiccation and anaerobic conditions on the behaviour, survival and general metabolism of three common cirripedes. *Journal of Animal Ecology*, **32**, 233-252.
- Barnes, M., 2000. The use of intertidal barnacle shells. *Oceanography and Marine Biology: an Annual Review*, **38**, 157-187.
- Baxter, J.M., 1997. *Aulacomya ater*: Magellan mussel: Moray Firth in Scotland in 1994 and again in 1997. *Joint Nature Conservation Committee*.
- Bayne, B., Iglesias, J., Hawkins, A., Navarro, E., Heral, M., Deslous-Paoli, J-M., 1993. Feeding behaviour of the mussel, *Mytilus edulis*: responses to variations in quantity and organic content of the seston. *Journal of the Marine Biological Association of the United Kingdom*, **73**, 813-29
- Bayne, B.L. (ed.), 1976b. *Marine mussels: their ecology and physiology*. Cambridge: Cambridge University Press. [International Biological Programme 10.]
- Bayne, B.L., Widdows, J. & Thompson, R.J., 1976. Physiological integrations. In *Marine mussels: their ecology and physiology* (ed. B.L. Bayne), pp. 261-299. Cambridge: Cambridge University Press. [International Biological Programme 10.]
- Beauchamp, K.A., Gowing, M.M., 1982. A quantitative assessment of human trampling effects on a rocky intertidal community. *Marine Environmental Research*, **7**, 279-94
- Beaumont, A., Abdul-Matin, A. & Seed, R., 1993. Early development, survival and growth in pure and hybrid larvae of *Mytilus edulis* and *M. galloprovincialis*. *Journal of Molluscan Studies*, **59**, 120-123.
- Beaumont, A.R., Gjedrem, T. & Moran, P., 2007. Blue mussel *Mytilus edulis* and Mediterranean mussel *M. galloprovincialis*. In T., S., et al. (eds.). Genetic impact of aquaculture activities on native populations. *GENIMPACT final scientific report (EU contract n. RICA-CT-2005-022802)*, pp. 62-69.
- Beaumont, A.R., Turner, G., Wood, A.R. & Skibinski, D.O.F., 2004. Hybridisations between *Mytilus edulis* and *Mytilus galloprovincialis* and performance of pure species and hybrid veliger larvae at different temperatures. *Journal of Experimental Marine Biology and Ecology*, **302** (2), 177-188.
- Beer, S. & Kautsky, L., 1992. The recovery of net photosynthesis during rehydration of three *Fucus* species from the Swedish West Coast following exposure to air. *Botanica Marina*, **35** (6), 487-492.
- Bellgrove, A., McKenzie, P.F., McKenzie, J.L. & Sfiligoj, B.J., 2010. Restoration of the habitat-forming furoid alga *Hormosira banksii* at effluent-affected sites: competitive exclusion by coralline turfs. *Marine Ecology Progress Series*, **419**, 47-56.
- Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B. & Slagstad, D. 2005. Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. *Marine Ecology Progress Series*, **303**, 167-175.
- Berger, R., Bergström, L., Granéli, E. & Kautsky, L., 2004. How does eutrophication affect different life stages of *Fucus vesiculosus* in the Baltic Sea? - a conceptual model. *Hydrobiologia*, **514** (1-3), 243-248.
- Berger, R., Henriksson, E., Kautsky, L. & Malm, T., 2003. Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquatic Ecology*, **37** (1), 1-11.
- Bergmann, M., Wieczorek, S.K., Moore, P.G., 2002. Utilisation of invertebrates discarded from the *Nephrops* fishery by variously selective benthic scavengers in the west of Scotland. *Marine Ecology Progress Series*, **233**, 185-98
- Bergström, L., Berger, R. & Kautsky, L., 2003. Negative direct effects of nutrient enrichment on the establishment of *Fucus vesiculosus* in the Baltic Sea. *European Journal of Phycology*, **38** (1), 41-46.
- Berthe, F.C.J., Le Roux, F., Adlard, R.D. & Figueras, A., 2004. Marteilioidosis in molluscs: a review. *Aquatic Living Resources*, **17** (4), 433-448.
- Bertness, M.D., Gaines, S.D., Bermudez, D. & Sanford, E., 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*, **75**, 91-100.
- Besten, P.J. den, Herwig, H.J., Zandee, D.I. & Voogt, P.A., 1989. Effects of Cd and PCBs on reproduction in the starfish *Asterias rubens*: aberrations in early development. *Ecotoxicology and Environmental Safety*, **18**, 173-180.
- Bierne, N., David, P., Boudry, P. & Bonhomme, F., 2002. Assortative fertilization and selection at larval stage in the mussels *Mytilus edulis* and *M. galloprovincialis*. *Evolution*, **56**, 292-298.
- Bishop, J. 2012c. Carpet Sea-squirt, *Didemnum vexillum*. *Great Britain Non-native Species Secretariat* [On-line]. [cited 30/10/2018]. Available from: <http://www.nonnativespecies.org/factsheet/factsheet.cfm?speciesId=1209>
- Bishop, J. 2015a. Compass sea squirt, *Asterocarpa humilis*. *Great Britain Non-native Species Secretariat*. [On-line] [cited 16/06/2015]. Available from: <http://www.nonnativespecies.org>
- Bishop, J. 2015b. *Watersipora subatra*. *Great Britain Non-native Species Secretariat*. [On-line][cited 16/06/2015]. Available from: <http://www.nonnativespecies.org>
- Bixler, H.J. & Porse, H., 2010. A decade of change in the seaweed hydrocolloids industry. *Journal of Applied Phycology*, **23** (3), 321-335.
- Blanchard, M., 1997. Spread of the slipper limpet *Crepidula fornicata* (L.1758) in Europe. Current state and consequences. *Scientia Marina*, **61**, Supplement 9, 109-118.
- Blanchette, C.A., 1997. Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. *Ecology*, **78** (5), 1563-1578.
- Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marba, N., Moy, F.E., Barrón, C., Bjerkgeng, B., Borum, J., Christie, H. & Engelbert, S., 2003.

- The response of experimental rocky shore communities to nutrient additions. *Ecosystems*, **6** (6), 577-594.
- Bokn, T.L., Moy, F.E. & Murray, S.N., 1993. Long-term effects of the water-accommodated fraction (WAF) of diesel oil on rocky shore populations maintained in experimental mesocosms. *Botanica Marina*, **36**, 313-319.
- Bokn, T.L., Moy, F.E., Christie, H., Engelbert, S., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Marba, N. & Pedersen, M.F., 2002. Are rocky shore ecosystems affected by nutrient-enriched seawater? Some preliminary results from a mesocosm experiment. *Sustainable Increase of Marine Harvesting: Fundamental Mechanisms and New Concepts*: Springer, pp. 167-175.
- Boller, M.L. & Carrington, E., 2006. In situ measurements of hydrodynamic forces imposed on *Chondrus crispus* Stackhouse. *Journal of Experimental Marine Biology and Ecology*, **337** (2), 159-170.
- Boller, M.L. & Carrington, E., 2007. Interspecific comparison of hydrodynamic performance and structural properties among intertidal macroalgae. *Journal of Experimental Biology*, **210** (11), 1874-1884.
- Bonner, T. M., Pyatt, F. B. & Storey, D. M., 1993. Studies on the motility of the limpet *Patella vulgata* in acidified sea-water. *International Journal of Environmental Studies*, **43**, 313-320.
- Boström, C. & Bonsdorff, E., 2000. Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series*, **205**, 123-138.
- Boulard, C. & Claereboudt, M.R., 1994. Effect of the castrating parasitic ciliate *Orchitophrya stellarum* on the population structure of *Asterias vulgaris*. In *Echinoderms through time* (ed. B. David, A. Guille, J.P. Féral & M. Roux), pp. 280. Rotterdam: A.A. Balkema.
- Bourget, E., 1983. Seasonal variations of cold tolerance in intertidal molluscs and their relation to environmental conditions in the St. Lawrence Estuary. *Canadian Journal of Zoology*, **61**, 1193-1201.
- Bousfield, E.L., 1973. *Shallow-water gammaridean Amphipoda of New England*. London: Cornell University Press.
- Bower S.M., 2010. Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish [online]. Ontario, Fisheries and Oceans, Canada. Available from: <http://dev-public.rhq.pac.dfo-mpo.gc.ca/science/species-especes/shellfish-coquillages/diseases-maladies/index-eng.htm> [Accessed: 14/02/2014]
- Bower, S.M., 2011. *Marteilia refringens/maurini* of Mussels [online]. Available from: <http://dev-public.rhq.pac.dfo-mpo.gc.ca/science/species-especes/shellfish-coquillages/diseases-maladies/pages/mrmaurmu-eng.htm> [Accessed: 05/03/2014]
- Bower, S.M. & McGladdery, S.E., 1996. Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish. *Sea Lane Diseases of Shellfish*. [on-line]. <http://www-sci.pac.dfo-mpo.gc.ca/sealane/aquac/pages/toc.htm>, 2000-11-27
- Bower, S.M., 1992. Diseases and parasites of mussels. In *The mussel Mytilus: ecology, physiology, genetics and culture* (ed. E.M. Gosling), pp. 543-563. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25.]
- Bowman, R.S. & Lewis, J.R., 1977. Annual fluctuations in the recruitment of *Patella vulgata* L. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 793-815.
- Brawley, S.H. & Johnson, L.E., 1991. Survival of fucoid embryos in the intertidal zone depends upon developmental stages and microhabitat. *Journal of Phycology*, **27** (2), 179-186.
- Brawley, S.H., 1992b. Mesoherbivores. In *Plant-animal interactions in the marine benthos* (ed. D.M John, S.J. Hawkins & J.H. Price), pp. 235-263. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]
- Brazier, P., Davies, J., Holt, R. & Murray, E., 1998. *Marine Nature Conservation Review Sector 5. South-east Scotland and north-east England: area summaries*. Peterborough: Joint Nature Conservation Committee. [Coasts and Seas of the United Kingdom. MNCR Series]
- Brosnan, D.M., 1993. The effect of human trampling on biodiversity of rocky shores: monitoring and management strategies. *Recent Advances in Marine Science and Technology*, **1992**, 333-341.
- Brosnan, D.M. & Crumrine, L.L., 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology*, **177**, 79-97.
- Brousseau, D.J., Goldberg, R. & Garza, C., 2014. Impact of Predation by the Invasive Crab *Hemigrapsus sanguineus* on Survival of Juvenile Blue Mussels in Western Long Island Sound. *Northeastern Naturalist*, **21** (1), 119-133.
- Brown, P.J. & Taylor, R.B., 1999. Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal. *Journal of Experimental Marine Biology and Ecology*, **235**, 45-53.
- Brown, V., Davies, S. & Synnot, R., 1990. Long-term monitoring of the effects of treated sewage effluent on the intertidal macroalgal community near Cape Schanck, Victoria, Australia. *Botanica Marina*, **33** (1), 85-98.
- Browne, M.A., Dissanayake, A., Galloway, T.S., Lowe, D.M. & Thompson, R.C., 2008. Ingested microscopic plastic translocates to the circulatory system of the mussel, *Mytilus edulis* (L.). *Environmental Science & Technology*, **42** (13), 5026-5031.
- Bryan, G.W. & Gibbs, P.E., 1983. *Heavy metals from the Fal estuary, Cornwall: a study of long-term contamination by mining waste and its effects on estuarine organisms*. Plymouth: Marine Biological Association of the United Kingdom. [Occasional Publication, no. 2.]
- Bryan, G.W. & Gibbs, P.E., 1991. Impact of low concentrations of tributyltin (TBT) on marine organisms: a review. In: *Metal ecotoxicology: concepts and applications* (ed. M.C. Newman & A.W. McIntosh), pp. 323-361. Boston: Lewis Publishers Inc.
- Bryan, G.W., 1984. Pollution due to heavy metals and their compounds. In *Marine Ecology: A Comprehensive, Integrated Treatise on Life in the Oceans and Coastal Waters*, vol. 5. *Ocean Management*, part 3, (ed. O. Kinne), pp.1289-1431. New York: John Wiley &

Sons.

Bryan, G.W., Langston, W.J., Hummerstone, L.G., Burt, G.R. & Ho, Y.B., 1983. An assessment of the gastropod *Littorina littorea* (L.) as an indicator of heavy metal contamination in United Kingdom estuaries. *Journal of the Marine Biological Association of the United Kingdom*, **63**, 327-345.

Bulleri, F. & Airoidi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology*, **42** (6), 1063-1072.

Bulleri, F. & Benedetti-Cecchi, L., 2008. Facilitation of the introduced green alga *Caulerpa racemosa* by resident algal turfs: experimental evaluation of underlying mechanisms. *Marine Ecology Progress Series*, **364**, 77-86.

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

Burrows, E.M., 1991. *Seaweeds of the British Isles. Volume 2. Chlorophyta*. London: British Museum (Natural History).

Buschbaum, C. & Saier, B., 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. *Journal of Sea Research*, **45**, 27-36

Bussell, J. A., Gidman, E. A., Causton, D. R., Gwynn-Jones, D., Malham, S. K., Jones, M. L. M., Reynolds, B. & Seed, R., 2008. Changes in the immune response and metabolic fingerprint of the mussel, *Mytilus edulis* (Linnaeus) in response to lowered salinity and physical stress. *Journal of Experimental Marine Biology and Ecology*, **358**, 78-85.

Cabral-Oliveira, J., Mendes, S., Maranhão, P. & Pardal, M., 2014. Effects of sewage pollution on the structure of rocky shore macroinvertebrate assemblages. *Hydrobiologia*, **726** (1), 271-283.

Carlson, R.L., Shulman, M.J. & Ellis, J.C., 2006. Factors Contributing to Spatial Heterogeneity in the Abundance of the Common Periwinkle *Littorina Littorea* (L.). *Journal of Molluscan Studies*, **72** (2), 149-156.

Chandrasekara, W.U. & Frid, C.L.J., 1998. A laboratory assessment of the survival and vertical movement of two epibenthic gastropod species, *Hydrobia ulvae*, (Pennant) and *Littorina littorea* (Linnaeus), after burial in sediment. *Journal of Experimental Marine Biology and Ecology*, **221**, 191-207.

Cohen A.N., 2011. *The Exotics Guide: Non-native Marine Species of the North American Pacific Coast*. [online]. Richmond, CA, Center for Research on Aquatic Bioinvasions. Available from: <http://www.exoticsguide.org> [Accessed: 20/03/2014]

Cole, S., Codling, I.D., Parr, W., Zabel, T., 1999. Guidelines for managing water quality impacts within UK European marine sites [On-line]. *UK Marine SACs Project*. [Cited 26/01/16]. Available from: http://www.ukmarinesac.org.uk/pdfs/water_quality.pdf

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.

Colhart, B.J., & Johanssen, H.W., 1973. Growth rates of *Corallina officinalis* (Rhodophyta) at different temperatures. *Marine Biology*, **18**, 46-49.

Commito, J.A., 1982. Effects of *Lunatia heros* predation on the population dynamics of *Mya arenaria* and *Macoma balthica* in Maine, USA. *Marine Biology*, **69**, 187-193.

Commito, J.A., 1987. Adult-larval interactions: predictions, mussels and cocoons. *Estuarine, Coastal and Shelf Science*, **25**, 599-606.

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

Connor, D.W., Brazier, D.P., Hill, T.O., & Northen, K.O., 1997b. Marine biotope classification for Britain and Ireland. Vol. 1. Littoral biotopes. *Joint Nature Conservation Committee, Peterborough, JNCC Report no. 229, Version 97.06., Joint Nature Conservation Committee, Peterborough, JNCC Report No. 230, Version 97.06.*

Connor, D.W., Dalkin, M.J., Hill, T.O., Holt, R.H.F. & Sanderson, W.G., 1997a. Marine biotope classification for Britain and Ireland. Vol. 2. Sublittoral biotopes. *Joint Nature Conservation Committee, Peterborough, JNCC Report no. 230, Version 97.06., Joint Nature Conservation Committee, Peterborough, JNCC Report no. 230, Version 97.06.*

Corradi, M.G., Gorbi, G. & Zanni, C., 2006. Hypoxia and sulphide influence gamete production in *Ulva* sp. *Aquatic Botany*, **84** (2), 144-150.

Craeymeersch, J.A., Herman, P.M.J. & Meire, P.M., 1986. Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (S.W. Netherlands). *Hydrobiologia*, **133**, 107-115.

Crisp, D.J. & Southward, A.J., 1961. Different types of cirral activity *Philosophical Transactions of the Royal Society of London, Series B*, **243**, 271-308.

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

Crompton, T.R., 1997. *Toxicants in the aqueous ecosystem*. New York: John Wiley & Sons.

Crossthwaite, S.J., Reid, N. & Sigwart, J.D., 2012. Assessing the impact of shore-based shellfish collection on under-boulder communities in Strangford Lough. *Report prepared by the Natural Heritage Research Partnership (NHRP) between Quercus, Queen's*

- University Belfast and the Northern Ireland Environment Agency (NIEA) for the Research and Development Series No. 13/03.
- Crothers, J., 1992. Shell size and shape variation in *Littorina littorea* (L.) from west Somerset. *Proceedings of the Third International Symposium on Littorinid Biology*, J. Grahame, P.J. Mill and D. G. Reid (eds.). *The Malacological Society of London*, pp. 91-97.
- Crothers, J.H., 1985. Dog-whelks: an introduction to the biology of *Nucella lapillus* (L.) *Field Studies*, **6**, 291-360.
- Culloty, S.C., Novoa, B., Pernas, M., Longshaw, M., Mulcahy, M.F., Feist, S.W. & Figueras, A., 1999. Susceptibility of a number of bivalve species to the protozoan parasite *Bonamia ostreae* and their ability to act as vectors for this parasite. *Diseases of Aquatic Organisms*, **37** (1), 73-80.
- Cummins, V., Coughlan, S., McClean, O., Connolly, N., Mercer, J. & Burnell, G., 2002. An assessment of the potential for the sustainable development of the edible periwinkle, *Littorina littorea*, industry in Ireland. *Report by the Coastal and Marine Resources Centre, Environmental Research Institute, University College Cork*.
- Daguin, C., Bonhomme, F. & Borsa, P., 2001. The zone of sympatry and hybridization of *Mytilus edulis* and *M. galloprovincialis*, as described by intron length polymorphism at locus mac-1. *Heredity*, **86**, 342-354.
- Daly, M.A. & Mathieson, A.C., 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology*, **43**, 45-55.
- Dame, R.F.D., 1996. *Ecology of Marine Bivalves: an Ecosystem Approach*. New York: CRC Press Inc. [Marine Science Series.]
- Dare, P.J., 1976. Settlement, growth and production of the mussel, *Mytilus edulis* L., in Morecambe Bay, England. *Fishery Investigations, Ministry of Agriculture, Fisheries and Food, Series II*, **28**, 25pp.
- Davenport, J. & Davenport, J.L., 2005. Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Marine Ecology Progress Series*, **292**, 41-50.
- Davenport, J., 1979. The isolation response of mussels (*Mytilus edulis*) exposed to falling sea water concentrations. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 124-132.
- Davenport, J., Moore, P.G., Magill, S.H. & Fraser, L.A., 1998. Enhanced condition in dogwhelks, *Nucella lapillus* (L.) living under mussel hummocks. *Journal of Experimental Marine Biology and Ecology*, **230**, 225-234.
- 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.
- Davies, G., Dare, P.J. & Edwards, D.B., 1980. Fenced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore crabs (*Carcinus maenas* (L.)) in Morecambe Bay, England. *Ministry of Agriculture, Fisheries and Food. Fisheries Technical Report*, no. 56.
- Davies, M.S., 1992. Heavy metals in seawater: effects on limpet pedal mucus production. *Water Research*, **26**, 1691-1693.
- Davies, S.P., 1970. Physiological ecology of *Patella* IV. Environmental and limpet body temperatures. *Journal of the Marine Biological Association of the United Kingdom*, **50** (04), 1069-1077.
- de Vooy, C.G.N., 1987. Elimination of sand in the blue mussel *Mytilus edulis*. *Netherlands Journal of Sea Research*, **21**, 75-78.
- 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.
- Denny, M.W., 1987. Lift as a mechanism of patch initiation in mussel beds. *Journal of Experimental Marine Biology and Ecology*, **113**, 231-45
- Devlinny, J. & Volsse, L., 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Marine Biology*, **48** (4), 343-348.
- Diaz, R.J. & Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review*, **33**, 245-303.
- Diederich, S., 2005. Differential recruitment of introduced Pacific oysters and native mussels at the North Sea coast: coexistence possible? *Journal of Sea Research*, **53** (4), 269-281.
- Diederich, S., 2006. High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **328** (2), 211-227.
- Dijkstra, J., Harris, L.G. & Westerman, E., 2007. Distribution and long-term temporal patterns of four invasive colonial ascidians in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology*, **342** (1), 61-68.
- Dinesen, G.E., Timmermann K., Roth E., Markager S., Ravn-Jonsen, L., Hjorth, M., Holmer M. & Støttrup J.G., 2011. Mussel Production and Water Framework Directive Targets in the Limfjord, Denmark: an Integrated Assessment for Use in System-Based Management. *Ecology & Society*, **16**(4). 26
- Dixon, P.S. & Irvine, L.M., 1977. *Seaweeds of the British Isles. Volume 1 Rhodophyta. Part 1 Introduction, Nemaliales, Gigartinales*. London: British Museum (Natural History) London.
- Dobretsov, S. & Wahl, M., 2008. Larval recruitment of the blue mussel *Mytilus edulis*: the effect of flow and algae. *Journal of Experimental Marine Biology and Ecology*, **355**, 137-44
- Doherty, S.D., Brophy, D. & Gosling, E., 2009. Synchronous reproduction may facilitate introgression in a hybrid mussel (*Mytilus*) population. *Journal of Experimental Marine Biology and Ecology*, **378**, 1-7.
- Dolmer, P. & Svane, I. 1994. Attachment and orientation of *Mytilus edulis* L. in flowing water. *Ophelia*, **40**, 63-74

- Dolmer, P., Kristensen, T., Christiansen, M.L., Petersen, M.F., Kristensen, P.S. & Hoffmann, E., 2001. Short-term impact of blue mussel dredging (*Mytilus edulis* L.) on a benthic community. *Hydrobiologia*, **465**, 115-127.
- Dolmer, P., Sand Kristensen, P. & Hoffmann, E., 1999. Dredging of blue mussels (*Mytilus edulis* L.) in a Danish sound: stock sizes and fishery-effects on mussel population dynamic. *Fisheries Research*, **40** (1), 73-80.
- Dommasnes, A., 1969. On the fauna of *Corallina officinalis* L. in western Norway. *Sarsia*, **38**, 71-86.
- Donkin, P., Widdows, J. & Evans, S.V., 1989. Quantitative structure activity relationships for the effect of hydrophobic organic chemicals on the rate of feeding of mussels. *Aquatic Toxicology*, **14**, 277-294.
- Dudgeon, S. R., Davison, L. R. & Vadas, R. L., 1989. Effect of freezing on photosynthesis of intertidal macroalgae relative tolerance of *Chondrus crispus* and *Mastocarpus stellatus* (Rhodophyta). *Marine Biology*, **101**, 107-114
- Dudgeon, S.R., Kuebler, J.E., Vadas, R.L. & Davison, I.R., 1995. Physiological responses to environmental variation in intertidal red algae: does thallus morphology matter? *Marine Ecology Progress Series*, **117**, 193-206.
- Ebere, A.G. & Akintonwa, A., 1992. Acute toxicity of pesticides to *Gobius* sp., *Palaemonetes africanus*, and *Desmocarisc trispimosa*. *Bulletin of Environmental Contamination and Toxicology*, **49**, 588-592.
- Edwards, E., 1997. Molluscan fisheries in Britain. In *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central American and Europe*, vol. 3, *Europe*, (ed. C.L. MacKenzie, Jr., V.G. Burrell, Jr., Rosenfield, A. & W.L. Hobart). *National Oceanic and Atmospheric Administration*, NOAA Technical Report NMFS 129.
- Ekaratne, S.U.K. & Crisp, D.J., 1984. Seasonal growth studies of intertidal gastropods from shell micro-growth band measurements, including a comparison with alternative methods. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 183-210.
- Emson, R.H., & Wilkie, I.C., 1980. Fission and autotomy in echinoderms. *Oceanography and Marine Biology: an Annual Review*, **18**, 155-250.
- Eno, N.C., Clark, R.A. & Sanderson, W.G. (ed.) 1997. *Non-native marine species in British waters: a review and directory*. Peterborough: Joint Nature Conservation Committee.
- Eriksson, B.K. & Bergström, L., 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. *Estuarine, Coastal and Shelf Science*, **62** (1), 109-117.
- Eriksson, B.K. & Johansson, G., 2003. Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *European Journal of Phycology*, **38** (3), 217-222.
- Eschweiler, N. & Buschbaum, C., 2011. Alien epibiont (*Crassostrea gigas*) impacts on native periwinkles (*Littorina littorea*). *Aquatic Invasions*, **6** (3), 281-290.
- Essink, K., 1999. Ecological effects of dumping of dredged sediments; options for management. *Journal of Coastal Conservation*, **5**, 69-80.
- Evans, R.G., 1948. The lethal temperatures of some common British littoral molluscs. *The Journal of Animal Ecology*, **17**, 165-173.
- Ewers, R., Kasperk, C. & Simmons, B., 1987. Biologisches Knochenimplantat aus Meeressalgen. *Zahnaerztliche Praxis*, **38**, 318-320.
- Feare, C.J., 1970b. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus*. *Oecologia*, **5**, 1-18.
- Firth, L., Thompson, R., Bohn, K., Abbiati, M., Airoidi, L., Bouma, T., Bozzeda, F., Ceccherelli, V., Colangelo, M. & Evans, A., 2014. Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. *Coastal Engineering*, **87**, 122-135.
- Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore*. Cambridge: Cambridge University Press.
- Floc'h, J. H. & Diouris, M., 1980. Initial effects of Amoco Cadiz oil on intertidal algae. *Ambio*, **9**, 284-286.
- Foster, B.A., 1970. Responses and acclimation to salinity in the adults of some balanomorph barnacles. *Philosophical Transactions of the Royal Society of London, Series B*, **256**, 377-400.
- Foster, B.A., 1971b. On the determinants of the upper limit of intertidal distribution of barnacles. *Journal of Animal Ecology*, **40**, 33-48.
- Frazer, A.W.J., Brown, M.T. & Bannister, P., 1988. The frost resistance of some littoral and sub-littoral algae from southern New Zealand. *Botanica Marina*, **31**, 461-464.
- Frechette, M., Butman, C.A., Geyer, W.R., 1989. The importance of boundary-layer flow in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnology and Oceanography*, **34**, 19-36.
- Fredersdorf, J., Müller, R., Becker, S., Wiencke, C. & Bischof, K., 2009. Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (Phaeophyceae). *Oecologia*, **160** (3), 483-492.
- Fretter, V. & Graham, A., 1994. *British prosobranch molluscs: their functional anatomy and ecology*, revised and updated edition. London: The Ray Society.
- Frieder, C., Nam, S., Martz, T. & Levin, L., 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences*, **9** (10), 3917-3930.
- Garbary, D.J., Beveridge, L.F., Flynn, A.D. & White, K.L., 2012. Population ecology of *Palmaria palmata* (Palmariales, Rhodophyta) from harvested and non-harvested shores on Digby Neck, Nova Scotia, Canada. *Algae*, **27** (1), 33-42.
- Gardner, J.P.A., 1996. The *Mytilus edulis* species complex in southwest England: effects of hybridization and introgression upon

- interlocus associations and morphometric variation. *Marine Biology*, **125**(2), 385-399.
- Gibbs, P.E., Green, J.C. & Pascoe, P.C., 1999. A massive summer kill of the dog-whelk, *Nucella lapillus*, on the north Cornwall coast in 1995: freak or forerunner? *Journal of the Marine Biological Association of the United Kingdom*, **79**, 103-109.
- Giltrap, M., Ronan, J., Hardenberg, S., Parkes, G., McHugh, B., McGovern, E. & Wilson, J., 2013. Assessment of biomarkers in *Mytilus edulis* to determine good environmental status for implementation of MSFD in Ireland. *Marine Pollution Bulletin*, **71** (1), 240-249.
- Glegg, G. A., Hickman, L. & Rowland, S. J., 1999. Contamination of limpets (*Patella vulgata*) following the Sea Empress oil spill. *Marine Pollution Bulletin*, **38**, 119-125.
- Gollety, C., Migne, A. & Davoult, D., 2008. Benthic metabolism on a sheltered rocky shore: Role of the canopy in the carbon budget. *Journal of Phycology*, **44** (5), 1146-1153.
- Gosling, E.M. (ed.), 1992a. *The mussel Mytilus: ecology, physiology, genetics and culture*. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]
- Gray, A.R., Lucas, I.A.N., Seed, R. & Richardson, C.A., 1999. *Mytilus edulis chilensis* infested with *Coccomyxa parasitica* (Chlorococcales, Coccomyxaceae). *Journal of Molluscan Studies*, **65**, 289-294.
- Gray, J.S., Wu R.S.-S. & Or Y.Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Series*, **238**, 249-279.
- Green, D., Chapman, M. & Blockley, D., 2012. Ecological consequences of the type of rock used in the construction of artificial boulder-fields. *Ecological Engineering*, **46**, 1-10.
- Grenon, J.F. & Walker, G., 1981. The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. *Journal of Experimental Marine Biology and Ecology*, **54**, 277-308.
- Groenewold, S. & Fonds, M., 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. *ICES Journal of Marine Science*, **57** (5), 1395-1406.
- Gruffydd, L.D., Huxley, R. & Crisp, D., 1984. The reduction in growth of *Mytilus edulis* in fluctuating salinity regimes measured using laser diffraction patterns and the exaggeration of this effect by using tap water as the diluting medium. *Journal of the Marine Biological Association of the United Kingdom* **64**: 401-9
- Gubbay, S., & Knapman, P.A., 1999. *A review of the effects of fishing within UK European marine sites*. Peterborough, English Nature.
- Guiry, M.D. & Guiry, G.M. 2015. AlgaeBase [Online], National University of Ireland, Galway [cited 30/6/2015]. Available from: <http://www.algaebase.org/>
- Gylle, A.M., Nygård, C.A. & Ekelund, N.G.A., 2009. Desiccation and Salinity Effects on Marine and Brackish *Fucus vesiculosus* L. (Phaeophyceae). *Phycologia*, **48** (3), 156-164.
- Hailey, N., 1995. Likely impacts of oil and gas activities on the marine environment and integration of environmental considerations in licensing policy. *English Nature Research Report*, no 145., Peterborough: English Nature.
- Hall, S.J., Basford, D.J. & Robertson, M.R., 1990. The impact of hydraulic dredging for razor clams *Ensis* spp. on an infaunal community. *Netherlands Journal of Sea Research*, **27**, 119-125.
- Hammann, M., Buchholz, B., Karez, R. & Weinberger, F., 2013. Direct and indirect effects of *Gracilaria vermiculophylla* on native *Fucus vesiculosus*. *Aquatic Invasions*, **8** (2), 121-132.
- Harding, J.M. & Mann, R., 1999. Observations on the biology of the Veined Rapa whelk, *Rapana whelk* (Valenciennes, 1846) in the Chesapeake Bay. *Journal of Shellfish Research*, **18**(1), 9-17.
- Harger, J.R.E. & Landenberger, D.E., 1971. The effects of storms as a density dependent mortality factor on populations of sea mussels. *The Veliger*, **14**, 195-210.
- Harlin, M.M., & Lindbergh, J.M., 1977. Selection of substrata by seaweed: optimal surface relief. *Marine Biology*, **40**, 33-40.
- Hartnoll, R.G. & Hawkins, S.J., 1985. Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia*, **24**, 53-63.
- Hartnoll, R.G., 1998. Circalittoral faunal turf biotopes: an overview of dynamics and sensitivity characteristics for conservation management of marine SACs, Volume VIII. *Scottish Association of Marine Sciences, Oban, Scotland*. [UK Marine SAC Project. Natura 2000 reports.]
- Hawkins, A., Smith, R., Bayne, B. & Heral, M., 1996. Novel observations underlying the fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis*. *Marine Ecology Progress Series*, **131**, 179-90
- Hawkins, S., 1983. Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology*, **71** (1), 55-72.
- Hawkins, S.J. & Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: an Annual Review*, **21**, 195-282.
- 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.
- 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.

- Herbert, R.J.H., Roberts, C., Humphreys, J., & Fletcher, S. 2012. The Pacific oyster (*Crassostrea gigas*) in the UK: economic, legal and environmental issues associated with its cultivation, wild establishment and exploitation. Available from: <http://www.dardni.gov.uk/pacific-oysters-issue-paper.pdf>
- Hickman, C.S., 1992. Reproduction and development of trochean gastropods. *Veliger*, **35**, 245-272.
- Hicks, G.R.F., 1985. Meiofauna associated with rocky shore algae. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.*, (ed. P.G. Moore & R. Seed, ed.). pp. 36-56. London: Hodder & Stoughton Ltd.
- Hillman, R.E., 1993. Relationship of environmental contaminants to occurrence of neoplasia in *Mytilus edulis* populations from east to west coast mussel-watch sites. *Journal of Shellfish Research*, **12**, 109.
- 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.
- Hiscock, K., 1984b. Sublittoral surveys of Bardsey and the Lleyn peninsula. August 13th to 27th, 1983. *Report prepared by the Field Studies Council, Oil Pollution Research Unit, Pembroke for the Nature Conservancy Council, CSD Report*, no. 612.
- Hoare, R. & Hiscock, K., 1974. An ecological survey of the rocky coast adjacent to the effluent of a bromine extraction plant. *Estuarine and Coastal Marine Science*, **2** (4), 329-348.
- Holmes, S.P., Walker, G. & van der Meer, J., 2005. Barnacles, limpets and periwinkles: the effects of direct and indirect interactions on cyprid settlement and success. *Journal of Sea Research*, **53** (3), 181-204.
- Holt, T.J., Hartnoll, R.G. & Hawkins, S.J., 1997. The sensitivity and vulnerability to man-induced change of selected communities: intertidal brown algal shrubs, *Zostera* beds and *Sabellaria spinulosa* reefs. *English Nature, Peterborough, English Nature Research Report No. 234*.
- 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.
- Holt, T.J., Rees, E.I., Hawkins, S.J. & Seed, R., 1998. Biogenic reefs (Volume IX). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. *Scottish Association for Marine Science (UK Marine SACs Project)*, 174 pp.
- Hong, J. & Reish, D.J., 1987. Acute toxicity of cadmium to eight species of marine amphipod and isopod crustaceans from southern California. *Bulletin of Environmental Contamination and Toxicology*, **39**, 884-888.
- Huff, T.M. & Jarett, J.K., 2007. Sand addition alters the invertebrate community of intertidal coralline turf. *Marine Ecology Progress Series*, **345**, 75-82.
- Hummel, H., Groeneveld, J.P., Nieuwenhuize, J., van Liere, J.M., Bogaards, R.H. & de Wolf, L., 1989. Relationship between PCB concentrations and reproduction in mussels *Mytilus edulis*. In *Fifth International Symposium on Responses of Marine Organisms to Pollutants*, 12-14 April 1989, Plymouth (ed. M.N. Moore & J. Stegeman). *Marine Environmental Research*, **28**, 489-493.
- Irvine, L. M. & Chamberlain, Y. M., 1994. *Seaweeds of the British Isles*, vol. 1. *Rhodophyta*, Part 2B *Corallinales*, *Hildenbrandiales*. London: Her Majesty's Stationery Office.
- Isaeus, M., 2004. Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. Department of Botany, Botaniska institutionen, Stockholm.
- Jenkins, S.R., Beukers-Stewart, B.D. & Brand, A.R., 2001. Impact of scallop dredging on benthic megafauna: a comparison of damage levels in captured and non-captured organisms. *Marine Ecology Progress Series*, **215**, 297-301.
- Jenner, H.A., Whitehouse, J.W., Taylor, C.J. & Khalanski, M. 1998. Cooling water management in European power stations Biology and control of fouling. *Hydroécologie Appliquée*, **10**, 1-225.
- JNCC, 2013. Blue Mussel Beds. Scottish MPA Project Fisheries Management Guidance, *Joint Nature Conservation Committee, Peterborough*, http://jncc.defra.gov.uk/pdf/SMPA_fisheries_management_guidance_blue_mussel_beds_July_2013.pdf
- 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>
- Johansen, W.H., 1974. Articulated coralline algae. *Oceanography and Marine Biology: an Annual Review*, **12**, 77-127.
- Johnson, W., Gigon, A., Gulmon, S. & Mooney, H., 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. *Ecology*, **55**: 450-453.
- Jones, N.S., 1951. The bottom fauna of the south of the Isle of Man. *Journal of Animal Ecology*, **20**, 132-144.
- Jones, S.J., Lima, F.P. & Wetthey, D.S., 2010. Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *Journal of Biogeography* **37**: 2243-59
- Jonsson, P.R., Granhag, L., Moschella, P.S., Åberg, P., Hawkins, S.J. & Thompson, R.C., 2006. Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology*, **87** (5), 1169-1178.
- Jorgensen, B.B., 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos*, **32**, 68-76.
- Jørgensen, C.B., 1981. Mortality, growth, and grazing impact on a cohort of bivalve larvae, *Mytilus edulis* L. *Ophelia*, **20**, 185-192.
- Kaiser, M.J. & Spencer, B.E., 1994. Fish scavenging behaviour in recently trawled areas. *Marine Ecology Progress Series*, **112** (1-2),

41-49.

Kamermans, P., Malta, E.-j., Verschuure, J.M., Lentz, L.F. & Schrijvers, L., 1998. Role of cold resistance and burial for winter survival and spring initiation of an *Ulva* spp.(Chlorophyta) bloom in a eutrophic lagoon (Veerse Meer lagoon, The Netherlands). *Marine Biology*, **131** (1), 45-51.

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

Karsten, U., Dummermuth, A., Hoyer, K. & Wiencke, C., 2003. Interactive effects of ultraviolet radiation and salinity on the ecophysiology of two Arctic red algae from shallow waters. *Polar Biology*, **26** (4), 249-258.

Kautsky, N., 1981. On the trophic role of the blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. *Kieler Meeresforschungen Sonderheft*, **5**, 454-461.

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

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

Kindig, A.C., & Littler, M.M., 1980. Growth and primary productivity of marine macrophytes exposed to domestic sewage effluents. *Marine Environmental Research*, **3**, 81-100.

Kinne, O. (ed.), 1971a. *Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters. Vol. 1 Environmental Factors, Part 2*. Chichester: John Wiley & Sons.

Kinne, O. (ed.), 1980. *Diseases of marine animals. vol. 1. General aspects. Protozoa to Gastropoda*. Chichester: John Wiley & Sons.

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

Kittner, C. & Riisgaard, H.U., 2005. Effect of temperature on filtration rate in the mussel *Mytilus edulis*: no evidence for temperature compensation. *Marine Ecology Progress Series* 305: 147-52

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

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

Kochmann, J., Buschbaum, C., Volkenborn, N. & Reise, K., 2008. Shift from native mussels to alien oysters: differential effects of ecosystem engineers. *Journal of Experimental Marine Biology and Ecology*, **364** (1), 1-10.

Koehn, R.K. & Hilbish, T.J., 1987. The biochemical genetics and physiological adaptation of an enzyme polymorphism. *American Scientist*, **75**, 134-141.

Koehn, R.K., 1983. Biochemical genetics and adaptation in molluscs. In *The Mollusca. vol. 2. Environmental biochemistry and physiology*, (ed. P.W. Hochachka), pp 305-330.

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

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

Kraufvelin, P., 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.

Lambert, G., 2004. The south temperate and Antarctic ascidian *Corella eumyota* reported in two harbours in north-western France. *Journal of the Marine Biological Association of the United Kingdom*, **84**, 239-241.

Lander, T.R., Robinson, S.M., MacDonald, B.A. & Martin, J.D., 2012. Enhanced growth rates and condition index of blue mussels (*Mytilus edulis*) held at integrated multitrophic aquaculture sites in the Bay of Fundy. *Journal of Shellfish Research*, **31** (4), 997-1007.

Landsberg, J.H., 1996. Neoplasia and biotoxins in bivalves: is there a connection? *Journal of Shellfish Research*, **15**, 203-230.

Langan R. & Howell W.H., 1994. Growth responses of *Mytilus edulis* to changes in water flow: A test of the "inhalant pumping speed" hypothesis. *Journal of Shellfish Research*, **13**(1), 289.

Last, K.S., Hendrick V. J, Beveridge C. M & Davies A. J, 2011. Measuring the effects of suspended particulate matter and smothering on the behaviour, growth and survival of key species found in areas associated with aggregate dredging. *Report for the Marine Aggregate Levy Sustainability Fund*,

Latham, H., 2008. Temperature stress-induced bleaching of the coralline alga *Corallina officinalis*: a role for the enzyme bromoperoxidase. *Bioscience Horizons*, 1-10

Lawrence, J.M., 1996. Mass mortality of echinoderms from abiotic factors. In *Echinoderm Studies Vol. 5* (ed. M. Jangoux & J.M. Lawrence), pp. 103-137. Rotterdam: A.A. Balkema.

Le Roux, F., Lorenzo, G., Peyret, P., Audemard, C., Figueras, A., Vivares, C., Gouy, M. & Berthe, F., 2001. Molecular evidence for the existence of two species of *Marteilia* in Europe. *Journal of Eukaryotic Microbiology*, **48** (4), 449-454.

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

- Leonard, G.H., Levine, J.M., Schmidt, P.R. & Bertness, M.D., 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology*, **79** (4), 1395-1411.
- Lewis, J., 1961. The Littoral Zone on Rocky Shores: A Biological or Physical Entity? *Oikos*, **12** (2), 280-301.
- Lewis, J. & Bowman, R.S., 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, **17** (2), 165-203.
- Lewis, J.R., 1977. The role of physical and biological factors in the distribution and stability of rocky shore communities. In *Proceedings of the 11th European Marine Biology Symposium, Galway, Ireland, 5-11 October 1976. Biology of Benthic Organisms* (ed. B.F. Keegan, P.O. C  idigh & P.J. Boaden), pp. 417-424. Oxford: Pergamon Press.
- 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.
- Lindahl, O. & Kollberg, S., 2008. How mussels can improve coastal water quality. *Bioscience Explained*, **5** (1), 1-14.
- 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.
- Littler, M. & Murray, S., 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Marine Biology*, **30** (4), 277-291.
- Littler, M.M., & Kauker, B.J., 1984. Heterotrichy and survival strategies in the red alga *Corallina officinalis* L. *Botanica Marina*, **27**, 37-44.
- Littler, M.M., Martz, D.R. & Littler, D.S., 1983. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Marine Ecology Progress Series*. **11** (2), 129-139.
- Liu, D.H.W. & Lee, J.M., 1975. Toxicity of selected pesticide to the bay mussel (*Mytilus edulis*). *United States Environmental Protection Agency*, EPA-660/3-75-016.
- Livingstone, D.R. & Pipe, R.K., 1992. Mussels and environmental contaminants: molecular and cellular aspects. In *The mussel Mytilus: ecology, physiology, genetics and culture*, (ed. E.M. Gosling), pp. 425-464. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]
- Long, D., 2006. BGS detailed explanation of seabed sediment modified Folk classification. Available from: http://www.emodnet-seabedhabitats.eu/PDF/GMHM3_Detailed_explanation_of_seabed_sediment_classification.pdf
- Long, J.D., Cochrane, E. & Dolecal, R., 2011. Previous disturbance enhances the negative effects of trampling on barnacles. *Marine Ecology Progress Series*, **437**, 165-173.
- Loo, L-O., 1992. Filtration, assimilation, respiration and growth of *Mytilus edulis* L. at low temperatures. *Ophelia* **35**: 123-31
- Loo, L-O. & Rosenberg, R., 1983. *Mytilus edulis* culture: Growth and production in western Sweden. *Aquaculture*, **35**, 137-150.
- Loosanoff, V.L., 1962. Effects of turbidity on some larval and adult bivalves. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **14**, 80-95.
- Lopez-Flores I., De la Herran, R., Garrido-Ramos, M.A., Navas, J.I., Ruiz-Rejon, C. & Ruiz-Rejon, M., 2004. The molecular diagnosis of *Marteilia refringens* and differentiation between *Marteilia* strains infecting oysters and mussels based on the rDNA IGS sequence. *Parasitology*, **19** (4), 411-419.
- L  ning, K., 1990. *Seaweeds: their environment, biogeography, and ecophysiology*: John Wiley & Sons.
- Luther, G., 1976. Bewuchsuntersuchungen auf Natursteinsubstraten im Gezeitenbereich des Nordsylder Wattenmeeres: Algen. *Helgol  nder Wissenschaftliche Meeresuntersuchungen*, **28** (3-4), 318-351.
- Lutz, R.A. & Kennish, M.J., 1992. Ecology and morphology of larval and early larval postlarval mussels. In *The mussel Mytilus: ecology, physiology, genetics and culture*, (ed. E.M. Gosling), pp. 53-85. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]
- Maddock, A., 2008. UK Biodiversity Action Plan; Priority Habitat Descriptions. *UK Biodiversity Action Plan*, 94pp
- Maggs, C.A. & Hommersand, M.H., 1993. *Seaweeds of the British Isles: Volume 1 Rhodophycota Part 3A Ceramiales*. London: Natural History Museum, Her Majesty's Stationary Office.
- Mainwaring, K., Tillin, H. & Tyler-Walters, H., 2014. Assessing the sensitivity of blue mussel beds to pressures associated with human activities. *Joint Nature Conservation Committee, JNCC Report No. 506.*, Peterborough, 96 pp.
- Malm, T. & Kautsky, L., 2003. Differences in life-history characteristics are consistent with the vertical distribution pattern of *Fucus serratus* and *Fucus vesiculosus* (Fucales, Phaeophyceae) in the central Baltic Sea. *Journal of Phycology*, **39** (5), 880-887.
- Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of seaweeds. *Marine Biology*, **12**, 1-10.
- Mann, R. & Harding, J.M., 2000. Invasion of the North American Atlantic coast by a large predatory Asian mollusc. *Biological Invasions*, **2** (1), 7-22.
- Mann, R. & Harding, J.M., 2003. Salinity tolerance of larval *Rapana venosa*: implications for dispersal and establishment of an invading predatory gastropod on the North American Atlantic coast. *The Biological Bulletin*, **204** (1), 96-103.
- Markert, A., Wehrmann, A. & Kr  ncke, I., 2010. Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological*

Invasions, **12** (1), 15-32.

Marshall, D.J. & McQuaid, C.D., 1989. The influence of respiratory responses on the tolerance to sand inundation of the limpets *Patella granularis* L.(Prosobranchia) and *Siphonaria capensis* Q. et G.(Pulmonata). *Journal of Experimental Marine Biology and Ecology*, **128** (3), 191-201.

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.

Mathieson, A.C. & Burns, R.L., 1975. Ecological studies of economic red algae. 5. Growth and reproduction of natural and harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. *Journal of Experimental Marine Biology and Ecology*, **17**, 137-156.

May, V., 1985. Observations on algal floras close to two sewerage outlets. *Cunninghamia*, **1**, 385-394.

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

McGrorty, S., Clarke, R.T., Reading, C.J. & Goss, C.J.D., 1990. Population dynamics of the mussel *Mytilus edulis*: density changes and regulation of the population in the Exe Estuary, Devon. *Marine Ecology Progress Series*, **67**, 157-169.

McKay, D.W., 1994. *Aulacomya ater* (Mollina, 1782) [Mollusca: Pelecypoda] collected from the Moray Firth. *Porcupine Newsletter*, **5**, 23.

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

McLusky, D.S., Bryant, V. & Campbell, R., 1986. The effects of temperature and salinity on the toxicity of heavy metals to marine and estuarine invertebrates. *Oceanography and Marine Biology: an Annual Review*, **24**, 481-520.

Van der Meer, J., 1987. Experimental hybridization of *Palmaria palmata* (Rhodophyta) from the northeast and northwest Atlantic Ocean. *Canadian Journal of Botany*, **65** (7), 1451-1458.

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.

Minchin, D. 2007. Rapid coastal survey for targeted alien species associated with floating pontoons in Ireland. *Aquatic Invasions*, **2**(1), 63-70.

Minchin, D. & Sides, E., 2006. Appearance of a cryptogenic tunicate, a *Didemnum* sp. fouling marina pontoons and leisure craft in Ireland *Aquatic Invasions*, **1**(3), 143-147.

Minchin, D., 1995. Recovery of a population of the flame shell, *Lima hians*, in an Irish bay previously contaminated with TBT. *Environmental Pollution*, **90**, 259-262.

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

Moore, J., Taylor, P. & Hiscock, K., 1995. Rocky shore monitoring programme. *Proceedings of the Royal Society of Edinburgh*, **103B**, 181-200.

Moore, P.G., 1977a. Inorganic particulate suspensions in the sea and their effects on marine animals. *Oceanography and Marine Biology: An Annual Review*, **15**, 225-363.

Morgan, K.C., Shacklock, P.F. & Simpson, F.J., 1980. Some aspects of the culture of *Palmaria palmata* in greenhouse tanks. *Botanica Marina*, **23**, 765-770.

Morgan, S.G., 1995. Life and death in the plankton: Larval mortality and adaptation. In *Ecology of marine invertebrate larvae*, (ed. L. McEdward), pp.279-322. Florida, USA, CRC Press.

Moss, B., Mercer, S., & Shearer, A., 1973. Factors Affecting the Distribution of *Himantalia elongata* (L.) S.F. Gray on the North-east Coast of England. *Estuarine and Coastal Marine Science*, **1**, 233-243.

Mrowicki, R.J., Maggs, C.A. & O'Connor, N.E., 2014. Does wave exposure determine the interactive effects of losing key grazers and ecosystem engineers? *Journal of Experimental Marine Biology and Ecology*, **461** (0), 416-424.

Mudge, S.M., Salgado, M.A. & East, J., 1993. Preliminary investigations into sunflower oil contamination following the wreck of the *M.V. Kimya*. *Marine Pollution Bulletin*, **26**, 40-44.

Myrand, B., Guderley, H. & Himmelman, J.H., 2000. Reproduction and summer mortality of blue mussels *Mytilus edulis* in the Magdalen Islands, southern Gulf of St. Lawrence. *Marine Ecology Progress Series* **197**: 193-207

Narvarte, M., González, R., Medina, A. & Avaca, M.S., 2011. Artisanal dredges as efficient and rationale harvesting gears in a Patagonian mussel fishery. *Fisheries Research*, **111** (1), 108-115.

Nehls, G. & Thiel, M., 1993. Large-scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: Do storms structure the ecosystems? *Netherlands Journal of Sea Research*, **31**, 181-187.

Nenonen, N.P., Hannoun, C., Horal, P., Hernroth, B. & Bergström, T., 2008. Tracing of norovirus outbreak strains in mussels collected near sewage effluents. *Applied and Environmental Microbiology*, **74** (8), 2544-2549.

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

Newell, R.I.E., 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North -

- Mid-Atlantic). Blue Mussel. [on-line] <http://www.nwrc.usgs.gov/wdb/pub/0169.pdf>, 2001-02-15
- 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.
- Nietsch, B., 2009. Messung der Zähigkeit der Makroalge *Fucus vesiculosus* an verschiedenen Standorten und Untersuchung der Auswirkungen auf die trophische Interaktion. Diploma Thesis, University of Kiel.
- Norton, T.A., 1992. Dispersal by macroalgae. *British Phycological Journal*, **27**, 293-301.
- O'Brien, P.J. & Dixon, P.S., 1976. Effects of oils and oil components on algae: a review. *British Phycological Journal*, **11**, 115-142.
- Olafsson, E.B., Peterson, C.H. & Ambrose, W.G. Jr., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology: an Annual Review*, **32**, 65-109
- Olsenz, J.L., 2011. Stress ecology in *Fucus*: abiotic, biotic and genetic interactions. *Advances in Marine Biology*, **59** (57), 37.
- Orton, J.H., 1914. Preliminary account of a contribution to an evaluation of the sea. *Journal of the Marine Biological Association of the United Kingdom*, **X**, 312-320.
- Padilla, D.K., 2010. Context-dependent impacts of a non-native ecosystem engineer, the Pacific Oyster *Crassostrea gigas*. *Integrative and Comparative Biology*, **50** (2), 213-225.
- Page, H. & Hubbard, D., 1987. Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. *Journal of Experimental Marine Biology and Ecology* **111**: 159-79
- Paine, R.T. & Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs*, **51**, 145-178.
- Paine, R.T., 1976. Biological observations on a subtidal *Mytilus californianus* bed. *Veliger*, **19**, 125-130.
- Palmer, D.L., Burnett, K., Whelpdale, P., 2007. Baseline Survey of Shellfish Resources in Lough Foyle. CEFAS, C2697, pp
- Parry, H., & Pipe, R., 2004. Interactive effects of temperature and copper on immunocompetence and disease susceptibility in mussels (*Mytilus edulis*). *Aquatic Toxicology* **69**: 311-25
- 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.
- Pernet, F., Tremblay, R. & Bourget E., 2003. Settlement success, spatial pattern and behavior of mussel larvae *Mytilus* spp. in experimental downwelling systems of varying velocity and turbulence. *Marine Ecology Progress Series*, **260**, 125-140.
- Petpiroon, S. & Dicks, B., 1982. Environmental effects (1969 to 1981) of a refinery effluent discharged into Littlewick Bay, Milford Haven. *Field Studies*, **5**, 623-641.
- Pieters, H., Klutymans, J.H., Zandee, D.I. & Cadée, G.C., 1980. Tissue composition and reproduction of *Mytilus edulis* dependent upon food availability. *Netherlands Journal of Sea Research*, **14**, 349-361.
- 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.
- Povey, A. & Keough, M.J., 1991. Effects of trampling on plant and animal populations on rocky shores. *Oikos*, **61**: 355-368.
- Price, H., 1982. An analysis of factors determining seasonal variation in the byssal attachment strength of *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom*, **62** (01), 147-155
- Provan, J., Murphy, S. & Maggs, C.A., 2005. Tracking the invasive history of the green alga *Codium fragile* ssp. *tomentosoides*. *Molecular Ecology*, **14**, 189-194.
- Purchon, R.D., 1937. Studies on the biology of the Bristol Channel. *Proceedings of the Bristol Naturalists' Society*, **8**, 311-329.
- Quadir, A., Harrison, P. & DeWreede, R., 1979. The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. *Phycologia*, **18** (1), 83-88.
- Raffaelli, D., 1982. Recent ecological research on some European species of *Littorina*. *Journal of Molluscan Studies*, **48** (3), 342-354.
- Raffaelli, D. & Hawkins, S., 1999. *Intertidal Ecology* 2nd edn.. London: Kluwer Academic Publishers.
- Ramsay, K., Kaiser, M.J. & Hughes, R.N. 1998. The responses of benthic scavengers to fishing disturbance by towed gears in different habitats. *Journal of Experimental Marine Biology and Ecology*, **224**, 73-89.
- Rankin, C.J. & Davenport, J.A., 1981. *Animal Osmoregulation*. Glasgow & London: Blackie. [Tertiary Level Biology].
- Rayment W.J., 2007. *Crepidula fornicata*. Slipper limpet. [online]. *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme* [On-line]. Plymouth: Marine Biological Association of the United Kingdom. Available from: <<http://www.marlin.ac.uk>>
- Read, K.R.H. & Cumming, K.B., 1967. Thermal tolerance of the bivalve molluscs *Modiolus modiolus* (L.), *Mytilus edulis* (L.) and *Brachidontes demissus* (Dillwyn). *Comparative Biochemistry and Physiology*, **22**, 149-155.
- Reed, R.H. & Russell, G., 1979. Adaptation to salinity stress in populations of *Enteromorpha intestinalis* (L.) Link. *Estuarine and Coastal Marine Science*, **8**, 251-258.
- Reid, G., Liutkus, M., Bennett, A., Robinson, S., MacDonald, B. & Page, F., 2010. Absorption efficiency of blue mussels (*Mytilus edulis* and *M. trossulus*) feeding on Atlantic salmon (*Salmo salar*) feed and fecal particulates: implications for integrated multi-trophic aquaculture. *Aquaculture*, **299** (1), 165-169.

- Ribeiro, P.A., Xavier, R., Santos, A.M. & Hawkins, S.J., 2009. Reproductive cycles of four species of *Patella* (Mollusca: Gastropoda) on the northern and central Portuguese coast. *Journal of the Marine Biological Association of the United Kingdom*, **89** (06), 1215-1221.
- Riemann B. & Hoffmann E., 1991. Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. *Marine Ecology Progress Series*, **69**(1), 171-178.
- Riisgård, H.U., Bøttiger, L. & Pleissner, D. 2012. Effect of salinity on growth of mussels, *Mytilus edulis*, with special reference to Great Belt (Denmark). *Open Journal of Marine Science*, **2**, 167-176
- Riisgård, H.U., Luskow, F., Pleissner, D., Lundgreen, K. & López, M., 2013. Effect of salinity on filtration rates of mussels *Mytilus edulis* with special emphasis on dwarfed mussels from the low-saline Central Baltic Sea. *Helgoland Marine Research*, **67**, 591-8
- Robbins, J.V., 1978. Effects of physical and chemical factors on photosynthetic and respiratory rates of *Palmaria palmata* (Florideophyceae). In *Proceedings of the ninth International Seaweed Symposium, Santa Barbara, California, USA, 20-27 August 1977*, (ed. Jensen, A. & Stein, J.R.), 273-283. Science Press, Princeton, NJ, USA.
- Robertson, A., 1991. Effects of a toxic bloom of *Chrysochromulina polylepis*, on the Swedish west coast. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 569-578.
- Robledo, J.A.F., Santarem, M.M., Gonzalez, P. & Figueras, A., 1995. Seasonal variations in the biochemical composition of the serum of *Mytilus galloprovincialis* Lmk. and its relationship to the reproductive cycle and parasitic load. *Aquaculture*, **133** (3-4), 311-322.
- Rohde, S., Hiebenthal, C., Wahl, M., Karez, R. & Bischof, K., 2008. Decreased depth distribution of *Fucus vesiculosus* (Phaeophyceae) in the Western Baltic: effects of light deficiency and epibionts on growth and photosynthesis. *European Journal of Phycology*, **43** (2), 143-150.
- Saier, B., 2002. Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. *Helgoland Marine Research*, **56**, 44-50
- Sanford, E., Bermudez, D., Bertness, M.D. & Gaines, S.D., 1994. Flow, food supply and acorn barnacle population dynamics. *Marine Ecology Progress Series*, **104**, 49-49.
- Schiel, D.R. & Foster, M.S., 1986. The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology: an Annual Review*, **24**, 265-307.
- 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.
- Schmidt, A.L. & Scheibling, R.E., 2007. Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. *Journal of Experimental Marine Biology and Ecology*, **341** (1), 110-130.
- Seed, R. & Suchanek, T.H., 1992. Population and community ecology of *Mytilus*. In *The mussel Mytilus: ecology, physiology, genetics and culture*, (ed. E.M. Gosling), pp. 87-169. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25.]
- Seed, R., 1969b. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores 2. Growth and mortality. *Oecologia*, **3**, 317-350.
- Seed, R., 1976. Ecology. In *Marine mussels: their ecology and physiology*, (ed. B.L. Bayne), pp. 81-120. Cambridge: Cambridge University Press.
- Seed, R., 1992. Systematics evolution and distribution of mussels belonging to the genus *Mytilus*: an overview. *American Malacological Bulletin*, **9**, 123-137.
- Seed, R., 1993. Invertebrate predators and their role in structuring coastal and estuarine populations of filter feeding bivalves. In *Proceedings of the NATO Advanced Research Workshop, Renesse, The Netherlands, November 30- December 4, 1992. Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes*, (ed. R.F. Dame), pp. 149-195. Berlin: Springer-Verlag.
- Seed, R., 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the United Kingdom*, **76**, 203-210.
- Serrao, E.A., Kautsky, L., Lifvergren, T. & Brawley, S.H., 1997. Gamete dispersal and pre-recruitment mortality in Baltic *Fucus vesiculosus*. *Phycologia*, **36**, 101-102.
- Serrão, E.A., Kautsky, L., Lifvergren, T. & Brawley, S.H., 2000. Gamete dispersal and pre-recruitment mortality in Baltic *Fucus vesiculosus* (Abstract only). *Phycologia*, **36** (Suppl.), 101-102.
- Sewell, J. 2011c. Wireweed, *Sargassum muticum*. *Great Britain Non-native Species Secretariat*. [cited 16/06/2015]. Available from: <<http://www.nonnativespecies.org>
- Sewell, J., Pearce, S., Bishop, J. & Evans, J.L., 2008. Investigations to determine the potential risk for certain non-native species to be introduced to North Wales with mussel seed dredged from wild seed beds. *CCW Policy Research Report*, **835**, 82 pp., Countryside Council for Wales
- Shanks, A.L. & Wright, W.G., 1986. Adding teeth to wave action- the destructive effects of wave-bourne rocks on intertidal organisms. *Oecologia*, **69** (3), 420-428.
- Shumway, S.E., 1990. A review of the effects of algal blooms on shellfish and aquaculture. *Journal of the World Aquaculture Society*, **21**, 65-104.
- Shumway, S.E., 1992. Mussels and public health. In *The mussel Mytilus: ecology, physiology, genetics and culture*, (ed. E. Gosling), pp.

- 511-542. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]
- Smaal, A.C., 2002. European mussel cultivation along the Atlantic coast: production status, problems and perspectives. *Hydrobiologia*, **484** (1-3), 89-98.
- Smaal, A.C. & Twisk, F., 1997. Filtration and absorption of *Phaeocystis* cf. *globosa* by the mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, **209**, 33-46
- Smith, G.M., 1947. On the reproduction of some Pacific coast species of *Ulva*. *American Journal of Botany*, **34**, 80-87.
- Smith, J.E. (ed.), 1968. 'Torrey Canyon'. *Pollution and marine life*. Cambridge: Cambridge University Press.
- Smith, J.R. & Murray, S.N., 2005. The effects of experimental bait collection and trampling on a *Mytilus californianus* mussel bed in southern California. *Marine Biology*, **147**, 699-706
- Southward, A.J. & Southward, E.C., 1978. Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. *Journal of the Fisheries Research Board of Canada*, **35**, 682-706.
- Southward, A.J., Hawkins, S.J. & Burrows, M.T., 1995. Seventy years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, **20**, 127-155.
- Stagnol, D., Renaud, M. & Davoult, D., 2013. Effects of commercial harvesting of intertidal macroalgae on ecosystem biodiversity and functioning. *Estuarine, Coastal and Shelf Science*, **130**, 99-110.
- Steen, H., 2004. Effects of reduced salinity on reproduction and germling development in *Sargassum muticum* (Phaeophyceae, Fucales). *European Journal of Phycology*, **39** (3), 293-299.
- Stephenson, T.A. & Stephenson, A., 1972. Life between tidemarks on rocky shores. *Journal of Animal Ecology*, **43** (2), 606-608.
- Stewart, J.G., 1989. Establishment, persistence and dominance of *Corallina* (Rhodophyta) in algal turf. *Journal of Phycology*, **25** (3), 436-446.
- Stickle, W.B. & Diehl, W.J., 1987. Effects of salinity on echinoderms. In *Echinoderm Studies, Vol. 2* (ed. M. Jangoux & J.M. Lawrence), pp. 235-285. A.A. Balkema: Rotterdam.
- Storey, K.B., Lant, B., Anozie, O.O. & Storey, J.M., 2013. Metabolic mechanisms for anoxia tolerance and freezing survival in the intertidal gastropod, *Littorina littorea*. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **165** (4), 448-459.
- Strömrgren, T., 1977. Short-term effect of temperature upon the growth of intertidal Fucales. *Journal of Experimental Marine Biology and Ecology*, **29**, 181-195.
- 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 of the indigenous macroalgal community. *Marine Ecology Progress Series*, **207**, 79-88.
- Suchanek, T.H., 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology*, **31**, 105-120.
- Suchanek, T.H., 1985. Mussels and their role in structuring rocky shore communities. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.*, (ed. P.G. Moore & R. Seed), pp. 70-96.
- Suchanek, T.H., 1993. Oil impacts on marine invertebrate populations and communities. *American Zoologist*, **33**, 510-523.
- Svåsand, T., Crosetti, D., García-Vázquez, E. & Verspoor, E., 2007. Genetic impact of aquaculture activities on native populations. *Genimpact final scientific report (EU contract n. RICA-CT-2005-022802)*.
- Sweet, N.S. 2011j. Green sea-fingers (tomentosoides), *Codium fragile* subsp. *tomentosoides*. *Great Britain Non-native Species Secretariat*. [cited 16/06/2015]. Available from: <<http://www.nonnativespecies.org>>
- Sweet, N.S. & Sewell, J. 2014. Asian shore crab, *Hemigrapsus sanguineus*. *Great Britain Non-native Species Secretariat*. [cited 16/06/2015]. Available from: <<http://www.nonnativespecies.org>>
- Tangen K., 1977. Blooms of *Gyrodinium aureolum* (Dinophyceae) in North European waters, accompanied by mortality in marine organisms. *Sarsia*, **6**, 123-33.
- Tasende, M.G. & Fraga, M.I., 1999. The growth of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinaceae) in laboratory culture. *Ophelia*, **51**, 203-213.
- Taskin, E., Ozturk, M. & Kurt, O., 2007. Antibacterial activities of some marine algae from the Aegean Sea (Turkey). *African Journal of Biotechnology*, **6** (24), 2746-2751.
- Tatarenkov, A., Bergström, L., Jönsson, R.B., Serrão, E.A., Kautsky, L. & Johannesson, K., 2005. Intriguing asexual life in marginal populations of the brown seaweed *Fucus vesiculosus*. *Molecular Ecology*, **14** (2), 647-651.
- Tatarenkov, A., Jönsson, R.B., Kautsky, L. & Johannesson, K., 2007. Genetic structure in populations of *Fucus vesiculosus* (Phaeophyceae) over spatial scales from 10 m to 800 km. *Journal of Phycology*, **43** (4), 675-685.
- Theede, H., Ponat, A., Hiroki, K. & Schlieper, C., 1969. Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Marine Biology*, **2**, 325-337.
- Theisen, B.F., 1982. Variation in size of gills, labial palps, and adductor muscle in *Mytilus edulis* L. (Bivalvia) from Danish waters. *Ophelia*, **21**, 49-63.
- Thieltges, D.W., 2005. Impact of an invader: epizootic American slipper limpet *Crepidula fornicata* reduces survival and growth in

- European mussels. *Marine Ecology Progress Series*, **286**, 13-19.
- Thieltges, D.W., Strasser, M. & Reise, K., 2003. The American slipper-limpet *Crepidula fornicata* (L.) in the Northern Wadden Sea 70 years after its introduction. *Helgoland Marine Research*, **57**, 27-33
- Thiesen, B.F., 1972. Shell cleaning and deposit feeding in *Mytilus edulis* L. (Bivalvia). *Ophelia*, **10**, 49-55.
- Thompson, G.A. & Schiel, D.R., 2012. Resistance and facilitation by native algal communities in the invasion success of *Undaria pinnatifida*. *Marine Ecology, Progress Series*, **468**, 95-105.
- Thompson, G.B., 1980. Distribution and population dynamics of the limpet *Patella vulgata* in Bantry Bay. *Journal of Experimental Marine Biology and Ecology*, **45**, 173-217.
- Thompson, I.S., Richardson, C.A., Seed, R. & Walker, G., 2000. Quantification of mussel (*Mytilus edulis*) growth from power station cooling waters in response to chlorination procedures. *Biofouling*, **16**, 1-15.
- Thompson, I.S., Seed, R., Richardson, C.A., Hui, L. & Walker, G., 1997. Effects of low level chlorination on the recruitment, behaviour and shell growth of *Mytilus edulis* Linnaeus in power station cooling water. *Scientia Marina*, **61** (Suppl. 2), 77-85.
- Torchin, M., Lafferty, K. & Kuris, A., 2002. Parasites and marine invasions. *Parasitology*, **124** (07), 137-151.
- Tracey, G.A., 1988. Effects of inorganic and organic nutrient enrichment on growth and bioenergetics of the blue mussel, *Mytilus edulis*. *Journal of Shellfish Research*, **7**, 562.
- Tsuchiya, M., 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. Caused by high temperature on rocky shores. *Journal of Experimental Marine Biology and Ecology* **66**: 101-11
- Tsuchiya, M. & Nishihira, M., 1985. Islands of *Mytilus* as a habitat for small intertidal animals: effect of island size on community structure. *Marine Ecology Progress Series*, **25**, 71-81.
- Tsuchiya, M. & Nishihira, M., 1986. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. *Marine Ecology Progress Series*, **31**, 171-178.
- Tyler-Walters, H., 2002. *Mytilus edulis* and *Fucus vesiculosus* on moderately exposed mid eulittoral rock. [online]. Plymouth, Marine Biological Association of the United Kingdom. Available from: <http://www.marlin.ac.uk/habitatbenchmarks.php?habitatid=46&code=2004> [Accessed: 05/03/2014]
- Tyler-Walters, H. & Arnold, C., 2008. Sensitivity of Intertidal Benthic Habitats to Impacts Caused by Access to Fishing Grounds. Report to Cynfor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN) [Contract no. FC 73-03-327], Marine Biological Association of the UK, Plymouth, 48 pp. Available from: www.marlin.ac.uk/publications
- Tyler-Walters, H. & Durkin, O., 2001. *Mytilus edulis* beds on variable salinity infralittoral mixed sediment. *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme Plymouth: Marine Biological Association of the United Kingdom*. (05/03/2014).
- UKTAG, 2014. UK Technical Advisory Group on the Water Framework Directive [online]. Available from: <http://www.wfduk.org>
- Vadas, R.L., Johnson, S. & Norton, T.A., 1992. Recruitment and mortality of early post-settlement stages of benthic algae. *British Phycological Journal*, **27**, 331-351.
- Vadas, R.L., Keser, M. & Rusanowski, P.C., 1976. Influence of thermal loading on the ecology of intertidal algae. In *Thermal Ecology II*, (eds. G.W. Esch & R.W. McFarlane), ERDA Symposium Series (Conf-750425, NTIS), Augusta, GA, pp. 202-212.
- Valentine, P.C., Carman, M.R., Blackwood, D.S. & Heffron, E.J., 2007. Ecological observations on the colonial ascidian *Didemnum* sp. in a New England tide pool habitat. *Journal of Experimental Marine Biology and Ecology*, **342** (1), 109-121.
- Van De Werfhorst L.C. & Pearse J.S., 2007. Trampling in the rocky intertidal of central California: a follow-up study. *Bulletin of Marine Science*, **81**(2), 245-254.
- Van der Meer, J. & Poeschel, C.M., 1985. *Petersenia palmariae* n. sp. (Oomycetes): a pathogenic parasite of the red alga *Palmaria mollis* (Rhodophyceae). *Canadian Journal of Botany*, **63** (3), 404-408.
- Van der Meer, J.P. & Chen, C.-M., 1979. Evidence for sexual reproduction in the red algae *Palmaria palmata* and *Halosaccion ramentaceum*.
- Vermaat J.E. & Sand-Jensen, K., 1987. Survival, metabolism and growth of *Ulva lactuca* under winter conditions: a laboratory study of bottlenecks in the life cycle. *Marine Biology*, **95** (1), 55-61.
- Vevers, H.G., 1951. The biology of *Asterias rubens* L. II. Parasitization of the gonads by the ciliate *Orchitophrya stellarum* Cepede. *Journal of the Marine Biological Association of the United Kingdom*, **29**, 619-624.
- 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.
- Wang, W. & Widdows, J., 1991. Physiological responses of mussel larvae *Mytilus edulis* to environmental hypoxia and anoxia. *Marine Ecology Progress Series*, **70**, 223-36
- Westerbom, M. & Jattu, S., 2006. Effects of wave exposure on the sublittoral distribution of blue mussels *Mytilus edulis* in a heterogeneous archipelago. *Marine Ecology Progress Series*, **306**, 191-200.
- Widdows J., Lucas J.S., Brinsley M.D., Salkeld P.N. & Staff F.J., 2002. Investigation of the effects of current velocity on mussel feeding and mussel bed stability using an annular flume. *Helgoland Marine Research*, **56**(1), 3-12.
- Widdows, J. & Donkin, P., 1992. Mussels and environmental contaminants: bioaccumulation and physiological aspects. In *The*

- mussel *Mytilus*: ecology, physiology, genetics and culture, (ed. E.M. Gosling), pp. 383-424. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]
- Widdows, J., 1991. Physiological ecology of mussel larvae. *Aquaculture*, **94**, 147-163.
- Widdows, J., Bayne, B.L., Livingstone, D.R., Newell, R.I.E. & Donkin, P., 1979a. Physiological and biochemical responses of bivalve molluscs to exposure to air. *Comparative Biochemistry and Physiology*, **62A**, 301-308.
- Widdows, J., Brinsley, M.D., Salkeld, P.N. & Elliott, M., 1998. Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface. *Estuaries*, **21**, 552-559.
- Widdows, J., Donkin, P. & Evans, S.V., 1987. Physiological responses of *Mytilus edulis* during chronic oil exposure and recovery. *Marine Environmental Research*, **23**, 15-32.
- Widdows, J., Donkin, P., Brinsley, M.D., Evans, S.V., Salkeld, P.N., Franklin, A., Law, R.J. & Waldock, M.J., 1995. Scope for growth and contaminant levels in North Sea mussels *Mytilus edulis*. *Marine Ecology Progress Series*, **127**, 131-148.
- Widdows, J., Moore, M., Lowe, D. & Salkeld, P., 1979b. Some effects of a dinoflagellate bloom (*Gyrodinium aureolum*) on the mussel, *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom*, **59** (2), 522-524.
- Wiedemann, T., 1994. *Oekologische Untersuchungen in Gezeitentümpeln des Helgolaender Nord-Ost Felswatts*. , Diploma thesis, University of Kiel, Germany.
- Williams, R.J., 1970. Freezing tolerance in *Mytilus edulis*. *Comparative Biochemistry and Physiology*, **35**, 145-161
- Winter, J., 1972. Long-term laboratory experiments on the influence of ferric hydroxide flakes on the filter-feeding behaviour, growth, iron content and mortality in *Mytilus edulis* L. *Marine pollution and sea life*. (ed. Ruvio, M.) London, England, pp. 392-396.
- Witman, J.D. & Suchanek, T.H., 1984. Mussels in flow: drag and dislodgement by epizoans. *Marine Ecology Progress Series*, **16** (3), 259-268.
- Wood, C., 2015. The red ripple bryozoan *Watersipora subatra*. *Great Britain Non-native Species Secretariat*. [On-line][cited 16/06/2015]. Available from: <http://www.nonnativespecies.org/factsheet/factsheet.cfm?speciesId=3748>
- Young, G.A., 1985. Byssus thread formation by the mussel *Mytilus edulis*: effects of environmental factors. *Marine Ecology Progress Series*, **24**, 261-271.
- Zandee, D.I., Holwerda, D.A., Kluytmans, J.H. & De Zwaan, A., 1986. Metabolic adaptations to environmental anoxia in the intertidal bivalve mollusc *Mytilus edulis* L. *Netherlands Journal of Zoology*, **36**(3), 322-343.
- Zander, C.D., 1986. Tripterygiidae. In *Fishes of the North-eastern Atlantic and the Mediterranean*, Vol. 3. (ed. P.J.P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen & E. Tortonese), pp. 1118-1121. Paris: UNESCO
- Zwaan de, A. & Mathieu, M., 1992. Cellular biochemistry and endocrinology. In *The mussel Mytilus: ecology, physiology, genetics and culture*, (ed. E.M. Gosling), pp. 223-307. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]