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Barnacles and *Littorina* spp. on unstable eulittoral mixed substrata

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

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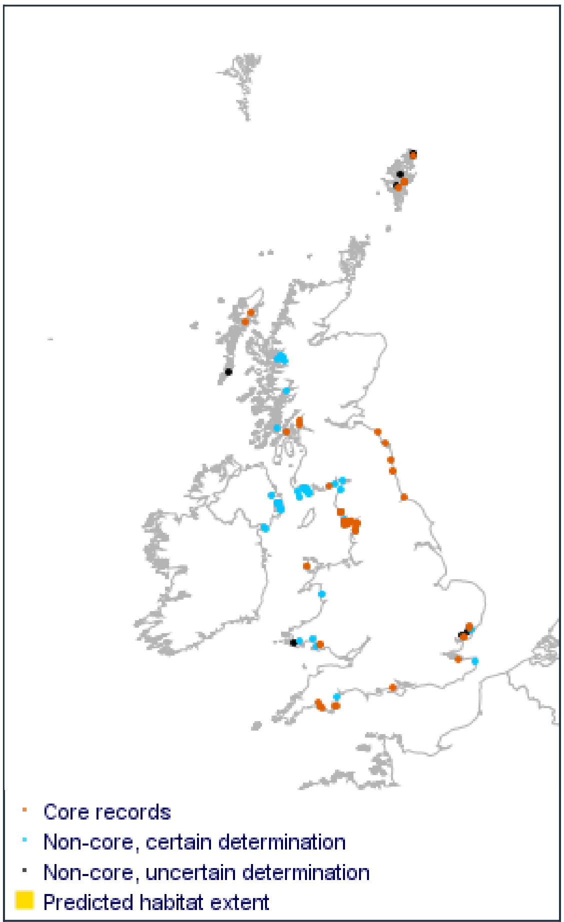
Boulder shore backed by low cliffs (SLR.BIlit)
Photographer: Paul Brazier



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

Researched by Dr Heidi Tillin & Jacqueline Hill **Refereed by** This information is not refereed.

Summary

UK and Ireland classification

EUNIS 2008	A2.431	Barnacles and *Littorina* spp. on unstable eulittoral mixed substrata
JNCC 2015	LR.FLR.Eph.BLitX	Barnacles and *Littorina* spp. on unstable eulittoral mixed substrata
JNCC 2004	LR.FLR.Eph.BLitX	Barnacles and *Littorina spp.* on unstable eulittoral mixed substrata
1997 Biotope	LR.SLR.FX.BLit	Barnacles and *Littorina littorea* on unstable eulittoral mixed substrata

Description

The eulittoral zone, particularly the mid shore zone, of sheltered to extremely sheltered mixed substrata shores is often characterized by flat banks or scards of cobbles and pebbles (on sediment) which are either too small or unstable to support a seaweed community. The boulders and larger cobbles are usually colonised by the barnacles *Semibalanus balanoides* or in areas with variable salinity *Elminius modestus* and often dense aggregations of the winkles *Littorina littorea* and *Littorina saxatilis* are present as well. Between the cobbles and pebbles the mussel *Mytilus edulis* occasionally occurs, but always at low abundance. Juvenile crabs *Carcinus maenas* and gammarids may occur between and underneath the pebbles and cobbles. Brown seaweeds are rare, although the wrack *Fucus vesiculosus* may occasionally occur on larger cobbles and small boulders in the mid and upper shore zones. Ephemeral green seaweeds such as *Ulva intestinalis* may also be present. Shallow pools and patches of standing water may occur in low-lying areas and may contain amphipods and filamentous green seaweeds. Due to the unstable nature of the substratum the diversity and density of flora and fauna is characteristically low (Information from Connor *et al*., 2004; JNCC, 2015).

Depth range

Mid shore

Additional information

None entered

Listed By

- none -

Further information sources

Search on:

G G G JNCC

Habitat review

Ecology

Ecological and functional relationships

- The SLR.BLlit biotope is found in a range of wave exposures. In exposed locations disturbance is high creating small scale succession events so that only fast growing opportunistic algal species such as *Ulva* are able to grow. However, the abundance of green algae in the biotope is low because of the grazing activity of *Littorina littorea* which occur in high abundance. In sheltered locations the substrata is more stable and fucoid sporelings may settle but are removed by the grazing activity of limpets and *Littorina littorea*. Thus, because of the impact of disturbance and/or grazing, algal cover is very low in the whole range of exposure in which the biotope is found.
- The pebble and cobble beaches of SLR.BLlit have a poor fauna in comparison to open shore locations on bedrock, presumably as a result of siltation and the instability of the substratum. There is a covering of barnacles on the cobbles and pebbles and on larger stable boulders and rock *Patella vulgata* is present in high abundance. *Littorina littorea*, which is tolerant of muddy and silty conditions, can be found in large aggregations and often cluster on the tops of small stones. Although *Mytilus edulis* is less common on cobbles and pebbles than on larger boulders or bedrock, the species may serve to enhance the stability of the substratum.
- Algal cover in the biotope is low and limited mostly to opportunistic green species such as *Ulva* spp. and *Ulva* spp.
- In extremely sheltered locations, even the smallest stones are relatively stable but remain unoccupied by algal sporelings so that barnacles settle (Lewis, 1964; Raffaelli & Hawkins, 1999).
- *Littorina littorea* is often the dominant grazing gastropod on the lower shore eating soft macrophytes and microalgae. Experiments in Helgoland (Janke, 1990) suggest that *Littorina* grazing can exclude the green alga *Ulva* and reduce the settlement and growth of *Fucus* species. Cover by opportunistic species like *Ulva* may be kept in check by littorinid grazing.
- A dense covering of barnacle species is effective in limiting the efficiency of limpet grazing which adversely affects limpet growth. Bulldozing by grazing limpets may cause high post-settlement mortality of barnacles (Jenkins *et al*., 2000).
- The crab *Carcinus maenas* is a predator of young *Littorina littorea*.
- The characterizing species of the sediment beneath the pebbles and cobbles are infaunal such as the obligate deposit feeding *Arenicola marina*.

Seasonal and longer term change

Rocky shore communities are often highly variable in time, due to the combined influences of physical disturbance, competition, grazing, predation and variation in recruitment. Barnacle dominated rocky shores demonstrate dynamic temporal changes, mediated by relatively random events such as recruitment intensity, and the abundance of grazers and predators (Hawkins *et al*., 1992; Raffaelli & Hawkins, 1999). Settlement of *Semibalanus balanoides* takes place in the spring and *Chthamalus* spp. in the summer and autumn. Seasonal fluctuations in the abundance of *Ulva* spp. may also be seen.

Habitat structure and complexity

Habitat complexity in this biotope is relatively limited in comparison to some rocky shore biotopes. However, the mixed nature of pebbles and cobbles, boulders, rocks and coarse sediment does create some complexity. Larger cobbles and boulders provide substratum and shelter for a variety of species such as small crabs and gammarid amphipods. Beneath boulders and the largest cobbles and pebbles (if free of sediment) underboulder communities may be present. Smaller pebbles and cobbles will be too small and too unstable (e.g. subject to overturn) for some encrusting species to persist.

Productivity

In the absence, or low abundance, of macroalgae, production in this biotope is mostly secondary production by suspension and deposit feeders. Primary production will be limited to microalgae growing on rock surfaces. Detrital input will be important for the suspension feeding barnacles and mussels. Rocky shores can make a contribution to the food of many marine species through the production of planktonic larvae and propagules which contribute to pelagic food chains. In general 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). However, in the SLR.BLlit biotope, faunal species may not attain the same biomass that may be found on stable rocky substrata on the open coast, so secondary productivity is likely to be lower.

Recruitment processes

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

- *Littorina littorea* can breed throughout the year but the length and timing of the breeding period are extremely dependent on climatic conditions. Also, estuaries provide a more nutritious environment than the open coast (Fish, 1972). Sexes are separate, and fertilisation is internal. *Littorina littorea* sheds egg capsules directly into the sea. Egg release is synchronized with spring tides and occurs on several separate occasions. In estuaries, the population matures earlier in the year and maximum spawning occurs in January (Fish, 1972). Fecundity value is up to 100,000 for a large female (27mm shell height) per year. Female fecundity increases with size. Larval settling time or pelagic phase can be up to six weeks. Males prefer to breed with larger, more fecund females (Erlandsson & Johannesson, 1992). Parasitism by trematodes may cause sterility in *Littorina littorea*.
- Barnacle settlement and recruitment can be highly variable because it is dependent on a suite of environmental and biological factors, such as wind direction and success depends on settlement being followed by a period of favourable weather. Long-term surveys have produced clear evidence of barnacle populations responding to climatic changes. During warm periods *Chthamalus* spp. Predominate, whilst *Semibalanus balanoides* does better during colder spells (Hawkins *et al*., 1994). Release of *Semibalanus balanoides* larvae takes place between February and April with peak settlement between April and June. Release

of larvae of *Chthamalus montagui* takes place later in the year, between May and August.
- Recruitment of *Patella vulgata* fluctuates from year to year and from place to place. Fertilization is external and the larvae is pelagic for up to two weeks before settling on rock at a shell length of about 0.2mm. Winter breeding occurs only in southern England, in the north of Scotland it breeds in August and in north-east England in September.
- *Mytilus edulis* recruitment is dependant on larval supply and settlement, together with larval and post-settlement 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.
- The infaunal polychaete *Arenicola marina* has high fecundity and the eggs develop lecithotrophically within the sediment or at the sediment surface. There is no pelagic larval phase and the juveniles disperse by burrowing. Recruitment must occur from local populations or by longer distance dispersal of postlarvae in water currents or during periods of bedload transport.
- *Ulva* is a rapidly growing opportunistic species which can colonize bare substrata soon after it is created.

Time for community to reach maturity

No specific information was found concerning time taken for the community to reach maturity. However, the characterizing species of the SLR.BLlit biotope are widespread, highly fecund and quick to grow and mature and so the community would be expected to reach maturity within 5 years. For example, Bennell (1981) observed that barnacles that were removed when the surface rock was scraped off in a barge accident at Amlwch, North Wales returned to pre-accident levels within 3 years. However, barnacle recruitment can be very variable because it is dependent on a suite of environmental and biological factors, such as wind direction, so populations may take longer to recruit to suitable areas. *Littorina littorea* is widespread and often common or abundant. *Littorina littorea* is an iteroparous breeder with high fecundity that lives for several (at least 4) years. Breeding can occur throughout the year and larvae form the main mode of dispersal. The planktonic larval stage is long (up to 6 weeks) although larvae do tend to remain in waters close to the shore. Most of the other species in the biotope have planktonic larvae and so should colonize suitable areas. Therefore, it seems likely that the biotope would reach maturity within five years. However, in newly created substrata, initial absence of grazing prosobranchs may allow first green, then brown algae to grow and dominate the shore until removed by scour or old age. In such cases the establishment of SLR.Bllit may take longer than five years.

Additional information

None

Preferences & Distribution

Habitat preferences

Depth Range	Mid shore
Water clarity preferences	Data deficient
Limiting Nutrients	Data deficient

Salinity preferences	Full (30-40 psu), Variable (18-40 psu)
Physiographic preferences	
Biological zone preferences	Eulittoral
Substratum/habitat preferences	Cobbles, Pebbles, Sand
Tidal strength preferences	No information
Wave exposure preferences	Extremely sheltered, Sheltered, Very sheltered
Other preferences	Unstable substrata

Additional Information

This biotope is found in a range of wave exposure regimes from exposed to extremely sheltered.

Species composition

Species found especially in this biotope

Rare or scarce species associated with this biotope

-

Additional information

None

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

The description of this biotope and information on the characterizing species is taken from Connor *et al*., (2004). The biotopes LR.FLR.Eph.EphX and LR.FLR.Eph.BLitX are very similar in terms of the species present and the habitats they occur in. The significant difference between these two variants is that the abundance of associated species (barnacles and littorinds) is greater in LR.FLR.Eph.BLitX and ephemeral green and red algae are present only in low abundances. Connor *et al*., (2004) suggest that LR.FLR.Eph.EphX may be a summer variation of LR.FLR.Eph.BLitX, in which ephemeral algal growth has exceeded the capacity of the grazing molluscs. The biotope is found on mixed substrata (pebbles and cobbles overlying sand or mud) where physical disturbance from sand abrasion, sediment instability or variable salinity, prevents the development of a longer-lived biological assemblage, such as the fucoid dominated biotopes, more typical of stable rocky shores or mixed substrata. The LR.FLR.Eph.BLitX biotope is characterized by flat banks or scards of cobbles and pebbles (on sediment) which are either too small or unstable to support a seaweed community. The boulders and larger cobbles are usually colonized by the barnacles *Semibalanus balanoides* or in areas with variable salinity *Elminius modestus* and often dense aggregations of the winkles *Littorina littorea* and *Littorina saxatilis* are present as well and sometimes *Mytilus edulis*, at low densities. Macroalgae may be present but at low densities due to the instability of the sediment. The mobile species may structure the assemblage through grazing on algae e.g. littorinids, or through predation on grazers, e.g. *Carcinus maenas*. Grazing by *Littorina littorea* can produce dramatic effects on both the algal assemblage (Lubchenco, 1978, 1983; Robles, 1982; Albrecht, 1998) and habitat structure (Bertness, 1984) of the intertidal zone.

The sensitivity assessments are based on the barnacles and littorinids which are considered to be the key characterizing species for this biotope; the littorinids are also considered to be a key structuring species through grazing. The sensitivity assessments also consider the general habitat characteristics of physically disturbed mixed substrata. The substratum mobility within this biotope may, however, be the key factor structuring the biotope. Where storms or wave action frequently move boulders and cobbles the scour and abrasion may crush and remove species or may result in them being in an unfavourable position. Barnacles and macroalgae that are present on an overturned boulder would be unable to feed or photosynthesise and would die.

Resilience and recovery rates of habitat

Where individuals are removed from a small area, littorinids may recolonize from surrounding patches of habitat where they are present. The recovery of the attached species *Semibalanus balanoides*, *Mytilus edulis* and the ephemeral algae will depend on recolonization by waterborne propagules. The characterizing and associated species are all common and widespread and reproduce annually producing pelagic larvae that can disperse over long distances. It is therefore likely that larval supply to impacted areas will provide high numbers of potential recruits. However, a range of factors, including species interactions, determine the rate of successful recruitment of juveniles to the population.

Semibalanus balanoides brood egg masses over autumn and winter and release the nauplii larvae during spring or early summer, to coincide with phytoplankton blooms on which the larvae feed. A range of local environmental factors, including surface roughness (Hills & Thomason, 1998), wind direction (Barnes, 1956), shore height, wave exposure (Bertness *et al*., 1991) and tidal currents

(Leonard *et al*., 1998) have been identified, among others, as affecting the settlement of *Semibalanus balanoides*. Biological factors such as larval supply, competition for space, presence of adult barnacles (Prendergast *et al*., 2009) and the presence of species that facilitate or inhibit settlement (Kendall *et al*., 1985, Jenkins *et al*., 1999) also play a role in recruitment. Mortality of juveniles can be high but highly variable, with up to 90 % of *Semibalanus balanoides* dying within ten days, therefore successful recruitment may be episodic (Kendall *et al*., 1985).

Barnacles are often quick to colonize available gaps, although a range of factors, as outlined above, will influence whether there is a successful episode of recruitment in a year to re-populate a shore following impacts. Bennell (1981) observed that barnacles that were removed when the surface rock was scraped off in a barge accident at Amlwch, North Wales returned to pre-accident levels within 3 years. Petraitis & Dudgeon (2005) also found that *Semibalanus balanoides* quickly recruited (present a year after and increasing in density) to experimentally cleared areas within the Gulf of Maine, that had previously been dominated by *Ascophyllum nodosum* However, barnacle densities were fairly low (on average 7.6 % cover) as predation levels in smaller patches were high and heat stress in large areas may have killed a number of individuals (Petraitis *et al*., 2003). Following creation of a new shore in the Moray Firth, *Semibalanus balanoides* did not recruit in large numbers until 4 years after shore creation (Terry & Sell, 1986).

Littorina littorea reproduces annually over an extended period, the egg capsules are shed directly into the sea. Egg release is synchronized with spring tides and occurs on several separate occasions. In estuaries, the population matures earlier in the year and maximum spawning occurs in January (Fish, 1972). A large female (27 mm shell height) may produce up to 100,000 egg capsules per year. Larval settling time or pelagic phase can be up to six weeks conferring high dispersal potential in the water column.

Resilience assessment. No evidence for recovery rates were found specifically for this biotope. Due to sediment instability this biotope is subject to frequent disturbance and the associated species assemblage is impoverished, consisting of few species that can either resist disturbances or recover rapidly through mortality or larval supply. The age structure of populations of the associated species is likely to be skewed towards young individuals due to high levels of mortality from disturbances. Most species, with the exception of littorinids are present at low abundances. Grazing by littorinids is a key factor structuring this biotope and their removal could lead to blooms of ephemeral algae (*Ulva* spp.) and biotope reclassification to LR.FLR.Eph.EphX. Biotope recovery to the normal state is considered to be rapid and resilience is assessed as ‘High’ (within 2 years) for all levels of resistance (None, Low, Medium and High).

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

Intertidal species 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 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 that the animal usually occurs at (Davenport & Davenport, 2005).

The median upper lethal temperature limit in laboratory tests on *Littorina saxatilis* and *Littorina littorea* collected in the summer at Great Cumbrae, Scotland), was approximately 35 °C (Davenport & Davenport, 2005). *Semibalanus balanoides* collected from the same shores had similarly high thermal tolerance, with summer collected individuals having a median upper lethal limit of approximately 35°C.

In laboratory experiments *Littorina littorea* collected from the Kiel Fjord in Germany and kept in tanks at temperatures 5°C above the seawater temperatures from the collection area (Kiel fjord, Germany) for 5 months (temperatures in laboratory ranged from 13-23°C) did not die although some decreases in shell strength were observed (Landes & Zimmer, 2012).

Although adults may be able to withstand acute and chronic increases in temperature at the pressure benchmark, increased temperatures may have sub-lethal effects on the population through impacts on reproduction. The distribution of the key characterizing species, *Semibalanus balanoides* is 'northern' with their range extending to the Arctic circle. Populations in the southern part of England are relatively close to the southern edge of their geographic range. Long-term time series show that successful recruitment of *Semibalanus balanoides* is correlated to sea temperatures (Mieszkowska, *et al*., 2014) and that due to recent warming its range has been contracting northwards. Temperatures above 10 to 12°C inhibit reproduction (Barnes, 1957, 1963; Crisp & Patel, 1969) and laboratory studies suggest that temperatures at or below 10°C for 4-6 weeks are required in winter for reproduction, although the precise threshold temperatures for reproduction are not clear (Rognstad *et al*., 2014). Observations of recruitment success in *Semibalanus balanoides* throughout the South West of England, strongly support the hypothesis that an extended period (4-6 weeks) of sea temperatures <10°C is required to ensure a good supply of larvae (Rognstad *et al*., 2014, Jenkins *et al*., 2000). During periods of high reproductive success, linked to cooler temperatures, the range of barnacles has been observed to increase, with range extensions in the order of 25 km (Wethey *et al*., 2011), and 100 km (Rognstad *et al*., 2014). Increased temperatures are likely to favour chthamalid barnacles or *Austrominius modestus* in the sheltered variable salinity biotopes rather than *Semibalanus balanoides* (Southward *et al*. 1995).

Most of the other species within the biotope are eurythermal (e.g. ephemeral algae *and Mytilus edulis*) and are also hardy intertidal species that tolerate long periods of exposure to the air and consequently wide variations in temperature. In addition, most species are distributed to the north of south of the UK and unlikely to be adversely affected by long-term temperature changes at the benchmark level.

Sensitivity assessment. Adult *Semibalanus balanoides* and *Littorina littorea* are considered likely to be able to tolerate an acute or chronic increase in temperature at the pressure benchmark, however, if an acute change in temperature occurred in autumn or winter it could disrupt reproduction in *Semibalanus balanoides* while a chronic change could alter reproductive success if it exceeded thermal thresholds for reproduction. The effects would depend on the magnitude, duration and footprint of the activities leading to this pressure. However, barnacle populations are highly connected, with a good larval supply and high dispersal potential (Wethey *et al*., 2011, Rognstad *et al*., 2014). The littorinids reproduce throughout the year and are not considered sensitive at the pressure benchmark. Resistance of the characterizing species is therefore assessed as 'High' and resilience as 'High' (by default). This biotope is, therefore, considered to be 'Not sensitive' at the pressure benchmark. Sensitivity to longer-term, broad-scale perturbations such as increased temperatures from climate change would however be greater, based on the extent of impact and the reduction in larval supply.

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 that the animal usually occurs at (Davenport & Davenport, 2005).

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. In experiments *Littorina littorea* were able to tolerate temperatures down to -8 °C for 8 days (Murphy, 1983). In colder conditions an active migration may occur down the shore to a zone where exposure time to the air (and hence time in freezing temperatures) is less

The distribution of the key characterizing species *Semibalanus balanoides* is 'northern' with their range extending to the Arctic circle. Over their range they are therefore subject to lower temperatures than in the UK, although distributions should be used cautiously as an indicator of thermal tolerance (Southward *et al*., 1995). Long-term time series show that recruitment success is correlated to lower sea temperatures (Mieszkowska *et al*., 2014). Due to warming temperatures its range has been contracting northwards. Temperatures above 10 to 12 °C inhibit reproduction (Barnes, 1957, 1963; Crisp & Patel, 1969) and laboratory studies suggest that temperatures at or below 10 °C for 4-6 weeks are required in winter for reproduction, although the precise threshold temperatures for reproduction are not clear (Rognstad *et al*., 2014).

The associated species *Mytilus edulis* and *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).

Sensitivity assessment. Based on the wide temperature tolerance range of *Littorina littorea* and other littorinids it is concluded that the acute and chronic decreases in temperature described by the benchmark would have limited effect. Similarly, based on global temperatures and the link between cooler winter temperatures and reproductive success, *Semibalanus balanoides* is also considered to be unaffected at the pressure benchmark. A decrease in temperature will favour *Semibalanus balanoides* over other barnacle species (Southward *et al*. 1995). Other species in the biotope also show low intolerance to decreases in temperate. long-term chronic temperature decreases may reduce growth. Therefore, a benchmark decrease in temperature is likely to result in sub-lethal effects only and this biotope is considered to have ‘High’ resistance and ‘High resilience (by default) to this pressure and is, therefore, considered to be ‘Not sensitive’.

Salinity increase (local)	High	High	Not sensitive
	Q: High A: High C: High	Q: High A: High C: High	Q: High A: High C: High

The biotope occurs in habitats subject to full and variable salinity (Connor et al., 2004). 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, these key characterizing species may be able to tolerate some increase in salinity. Resistance from a change to variable to full salinity is therefore assessed as ‘High’ and resilience is assessed as ‘High’ so that the biotope is ‘Not sensitive’.

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

The biotope occurs in subject to full and variable salinity (Connor *et al*., 2004). Evidence on salinity tolerances was found for the characterizing barnacle species. *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 reduces salinity the Australian barnacle *Austrominius* (formerly *Elminius*) *modestus* may be favoured, as this species is more tolerant of lower salinities and is found further up estuaries than other barnacles (Gomes-Filho *et al*., 2010).

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 at the pressure benchmark.

Similarly, most of the associated species (e.g. *Mytilus edulis)* are found in a wide range of salinities and are probably tolerant of variable or reduced salinity. A prolonged reduction in salinity, e.g. to reduced salinity (18-30 ppt) is likely to reduce the species richness of the biotope due to loss of some intolerant invertebrates. However, the dominant species will probably survive and the integrity of the biotope is likely to be little affected although some reduction in abundance may occur and this may be followed by an increase in ephemeral algae.

Sensitivity assessment. Based on reported distributions and the results of experiments to assess salinity tolerance thresholds and behavioural and physiological responses in *Littorina littorea* and *Semibalanus balanoides* it is considered that the benchmark decrease in salinity (from full to variable or variable to reduced) would not result in mortality of *Littorina littorea* and *Semibalanus balanoides* is judged to tolerate a change in salinity from full to variable but that a change from variable to reduced salinity may reduce habitat suitability and lead to replacement by *Austrominius modestus*. This replacement would not alter the character of the biotope. 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)	High Q: High A: Medium C: High	High Q: High A: High C: High	Not sensitive Q: High A: Medium C: High

The biotope is characteristic of areas sheltered from wave exposure that are subject to tidal streams. 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.

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 (3 m/s) 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 shell apertures are small to inhibit predation where *Carcinus maenas* is more prevalent while 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. Based on the available evidence the characterizing species *Littorina littorea* and *Semibalanus balanoides* are able to adapt to high flow rates and the biotope is, therefore, considered to be 'Not sensitive' to an increase in water flow. A decrease in water flow may have some effects on recruitment and growth, but this is not considered to be lethal at the pressure benchmark and resistance is therefore assessed as 'High' and resilience as 'High' by default. Changes in water flow may, however have impacts on the mixed substrata biotope. Reductions in flow may lead to increased deposition of silts and alter the sediment character, littorinids are found on sediments and may survive some deposition but barnacles would incur extra energetic costs filtering and clearing feeding apparatus. An increase in water flow at the pressure benchmark may re-suspend and remove sand particles which are less cohesive than mud particles. 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).Where these are protected by banks of cobbles and pebbles that protect the underlying sediment and reduce flow through friction the biotope will remain unchanged. The level of impact will depend on site specific hydrodynamic and sediment conditions. Biotope resistance to changes in water flow that do not alter the substrata is assessed as 'High' and resilience as 'High' (by default) so that the biotope is assessed as 'Not sensitive'

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

Emergence regime is a key factor structuring this (and other) intertidal biotopes. Records suggest that, typically, above this biotope is either the biotope dominated by ephemeral green seaweeds (LR.FLR.Eph.EphX), or, if it is found in the upper shore region, salt marsh species such as *Salacornia* and *Spartina* sp. Below are biotopes dominated by the wracks *Fucus serratus* or *Fucus vesiculosus*.

Increased emergence may reduce habitat suitability for characterizing species through greater exposure to desiccation and reduced feeding opportunities for the barnacles to feed when immersed. The mobile species present within the biotope, including the shore crab *Carcinus maenas* and the littorinids would be able to relocate to preferred shore levels. An increase in emergence that reduced habitat suitability for the grazing littorinids would allow blooms of ephemeral *Ulva* spp. to develop altering the classification of the biotope to LR.FLR.Eph.EphX.

Decreased emergence would reduce desiccation stress and allow the attached suspension feeding barnacles more feeding time. Predation pressure on mussels, littorinids and barnacles is likely to increase where these are submerged for longer periods and to prevent colonisation of lower zones. *Semibalanus balanoides* was able to extend its range into lower zones when protected from predation by the dogwhelk, *Nucella lapillus* (Connell, 1961) indicating that predation is a key factor setting the lower limit for this species. Competition from large fucoids and red algal turfs can also prevent *Semibalanus balano*ides from extending into lower shore levels (Hawkins, 1983). Decreased emergence is likely to lead to the habitat becoming more suitable for the lower shore species generally found below the biotope, leading to replacement, although the stability of the sediment will mediate the development of fucoid biotopes.

Sensitivity assessment. This biotope occurs on the mid-shore and will be sensitive to increased and decreased emergence. As emergence is a key factor structuring the distribution of animals and macroalgae on the shore, resistance to a change in emergence (increase or decrease) is assessed as 'Low'. Recovery is assessed as 'High', (following habitat recovery) and sensitivity is, therefore, assessed as 'Low'.

Wave exposure changes (local)	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 the sensitivity of this biotope to changes in wave exposure at the pressure benchmark. This biotope is recorded from locations that are judged to range from sheltered and moderately sheltered to extremely sheltered (Connor *et al*., 2004). The degree of wave exposure influences wave height, as in more exposed areas with a longer fetch waves would be predicted to be higher. As this biotope occurs across three wave exposure categories, this was therefore considered to indicate, by proxy, that biotopes in the middle of the wave exposure range would tolerate either an increase or decrease in significant wave height at the pressure benchmark.

An increase in wave action, exceeding the pressure benchmark, may however alter the character of the biotope. The cobbles and pebbles in the biotope are likely to move much more as a result of increased wave oscillation. The characterizing and associated species would probably accrue damage from abrasion and scour and barnacles trapped on the undersides of overturned pebbles would be unable to feed or respire. 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). *Littorina littorea* regularly have to abandon optimal feeding sites in order to avoid wave-induced dislodgement. This will result in a decreased growth rate (Mouritsen *et al*., 1999). Increases in wave exposure above the pressure benchmark will probably cause a decrease in population size of *Littorina littorea* and *Semibalanus balanoides.*

Sensitivity assessment. The natural wave exposure range of this biotope is considered to exceed changes at the pressure benchmark and this biotope is considered to have 'High' resistance and 'High' resilience (by default), to this pressure (at the benchmark).

Chemical Pressures

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

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

Contamination at levels greater than the benchmark may impact this biotope. However, barnacles, may tolerate fairly high level of heavy metals in nature, for example they possess metal detoxification mechanisms and are found in Dulas Bay, Anglesey, where copper reaches concentrations of 24.5 µg/l, due to acid mine waste (Foster *et al*., 1978; Rainbow, 1984). Bryan (1984) suggested that gastropods are also rather tolerant of heavy metals. *Littorina littorea* is tolerant of high TBT levels (Oehlmann *et al*., 1998) and has been found to be well suited for TBT effect monitoring because the species exists in sufficient numbers for sampling even in regions where a relatively high level of contamination exists. It is often present in areas where the very TBT sensitive dogwhelk *Nucella lapillus* has disappeared. Although imposex is rare in *Littorina littorea* strong TBT-toxication may affect a population significantly by reducing reproductive ability (Deutsch & Fioroni, 1996) through the development of intersex. Intersex is defined as a change in the female pallial oviduct towards a male morphological structure (Bauer *et al*., 1995). However, only sexually immature and juvenile individuals of *Littorina littorea* are able to develop intersex. Also, owing to the reproductive strategy of *Littorina littorea*, which reproduces by means of pelagic larvae, populations do not necessarily become extinct as a result of intersex (Casey *et al*., 1998) and so recoverability is good. It may take some time for the toxicant to be eliminated from the system and conditions to return to normal.

Littorina littorea has been suggested as a suitable bioindicator species for some heavy metals in the marine environment. Bryan *et al*. (1983) suggests that the species is a reasonable indicator for Ag, Cd, Pb and perhaps As. It is not found to be a reliable indicator for other metals because of some interactions between metals and regulation of some, such as Cu and Zn (Langston & Zhou Mingjiang, 1986).

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.

Littoral barnacles (e.g. *Semibalanus balanoides*) have a high resistance to oil (Holt *et al.*, 1995) but may suffer some mortality due to the smothering effects of thick oil (Smith, 1968).

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.

Synthetic compound contamination, at levels greater than the benchmark, is likely to have a variety of effects depending the specific nature of the contaminant and the species group(s) affected. Barnacles have a low resilience to chemicals such as dispersants, dependant on the concentration and type of chemical involved (Holt *et al.*, 1995).

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

No evidence was found.

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

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). *Littorina littorea* have a high tolerance for low oxygen conditions and can easily survive 3-6 days of anoxia (Storey *et al.*, 2013). In addition, *Littorina littorea*, is an air breather when emersed, so can respire during the tidal cycle.

Sensitivity assessment. The key characterizing species, littorinids and *Semibalanus balanoides* are considered to be 'Not Sensitive' to de-oxygenation at the pressure benchmark. The experiments cited as evidence (Storey *et al.*, 2013 and Barnes *et al.*,1963) exceed the duration and/or magnitude of the pressure benchmark and do not take into account the environmental mitigation of deoxygenation occurring in this biotope. Biotope resistance is therefore 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: Medium C: High	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

No direct evidence was found to assess this pressure. A slight increase in nutrient levels could be beneficial for barnacles and mussels by promoting the growth of phytoplankton levels and therefore increasing zooplankton levels. However, Holt *et al.* (1995) predict that smothering of barnacles by ephemeral green algae is a possibility under eutrophic conditions.

Littorina littorea occurs on all British and Irish coasts, including lower salinity areas such as this estuarine biotope where nutrient loading is likely to be higher than elsewhere. Higher nutrient levels may benefit the algal substrata and food used by the snail. In situations with nutrient enrichment, primary productivity in terms of biofilms and/ or green algae will generally be enhanced, which may supply more food or more nutrient rich food. This can reduce the browsing distances and periods of *Littorina*, reducing times spent searching for food (Diaz *et al*. 2012). After five months of nutrient addition in experimental mesocosms, *Littorina* abundance and biomass had increased compared to controls. Enriched mesocosms experiments were treated with 32 IM inorganic nitrogen (N) and 2 IM inorganic phosphorus (P) above the background levels in the Oslofjord continuously in the period April–September 2008. These nutrient addition levels are similar to concentrations recorded in eutrophic areas locally (Kristiansen & Paasche, 1982; cited in Diaz *et al*. 2012) and globally (Cloern, 2001; cited in Diaz *et al*. 2012).

Sensitivity assessment. The pressure benchmark is set at a level that is relatively protective and based on the evidence and considerations outlined above the biological assemblage is considered to be 'Not sensitive' at the pressure benchmark. Resistance and resilience are therefore assessed as 'High'.

Organic enrichment	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

Organic enrichment may lead to eutrophication with adverse environmental effects including deoxygenation, algal blooms and changes in community structure (see nutrient enrichment and de-oxygenation). The biotopes occurs in tide swept or wave exposed areas (Connor *et al.*, 2004) preventing a build up of organic matter, so that the biotope is considered to have a low risk of organic enrichment at the pressure benchmark. Little evidence was found to support this assessment, Cabral-Oliveira *et al.*, (2014), found that filter feeders such as *Mytilus* sp. and the barnacle *Chthamalus montagui* were more abundant at sites closer to a sewage treatment works, as they could utilise the organic matter inputs as food.

Sensitivity assessment. Little empirical evidence was found to support an assessment for *Semibalanus balanoides* and none for *Littorina littorea* within this biotope. As organic matter particles in suspension or re-suspended could potentially be utilised as a food resource by filter feeders present within the biotope (Cabral-Oliveira *et al.*, 2014), overall resistance of the biological assemblage within the biotope is considered to be 'High' and resilience was assessed as 'High', so that this biotope is judged to be 'Not sensitive'.

Physical Pressures

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

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

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

This biotope is characterized by the hard rock substratum provided by the boulders and cobbles to which the key characterizing species barnacles, limpets and littorinids and the other associated species can firmly attach. Littorinids are found on a variety of shores, including sedimentary so a change in type may not significantly affect this species. A change to a sedimentary substratum would, however, significantly alter the character of the biotope. 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, a similar effect would be predicted for barnacles and other animals within the biotope. The biotope is considered to have '**No**' resistance to this pressure based on a change to a soft sediment substratum, resilience is **Very low** (the pressure is a permanent change) and sensitivity is assessed as **High**. Although no specific evidence is described, confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

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

Not relevant to biotopes occurring on bedrock or on mixed substrata consisting of boulders, cobbles and pebbles.

Habitat structure changes - removal of substratum (extraction)	None Q: Low A: NR C: NR	High Q: High A: High C: High	Medium Q: Low A: Low C: Low

Extraction of the boulders, cobbles and pebbles on which this biotope occurs would remove the characterizing species and their habitat. Resistance is assessed as 'None' and resilience (following habitat recovery) is assessed as 'High'. Sensitivity is therefore assessed as 'Medium'.

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

The key characterizing and associated species within this biotope typically occur on the rock surfaces where they will be exposed to abrasion. Although barnacles and littorinids are protected by hard shells or plates, abrasion may damage and kill individuals or detach these. All removed barnacles would be expected to die as there is no mechanism for these to reattach. Although 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 are 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 appears to be variable with some studies not detecting significant differences between trampled and controlled areas (Tyler-Walters & Arnold, 2008). However, this variability may be related to differences in trampling intensities and abundance of populations studied. The worst case incidence was reported by Brosnan & Crumrine (1994) who reported that a trampling pressure of 250 steps in a 20x20 cm plot one day a month for a period of a year significantly reduced barnacle cover at two study sites. Barnacle cover reduced from 66 % to 7 % cover in 4 months at one site and from 21 % to 5 % within 6 months at the second site. Overall barnacles were crushed and removed by trampling. Barnacle cover remained low until recruitment the following spring. Long *et al*. (2011) also found that heavy trampling (70 humans /km/hrs) led to reductions in barnacle cover.

Single step experiments provide a clearer, quantitative indication of sensitivity to direct abrasion. Povey & Keough (1991) in experiments on shores in Mornington peninsula, Victoria, Australia, found that in single step experiments 10 out of 67 barnacles, (*Chthamlus antennatus* about 3mm long), were crushed.

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. The impact of surface abrasion will depend on the footprint, duration and magnitude of the pressure. Based on evidence from the step experiments and the relative robustness of these species, resistance, to a single abrasion event is assessed as 'Medium' and recovery as 'High', so that sensitivity is assessed as 'Low'. Resistance will be lower (and hence sensitivity greater) to abrasion events that exert a greater crushing force than the trampling examples the assessment is based on).

Penetration or disturbance of the substratum subsurface	Low Q: High A: Low C: NR	High Q: High A: High C: High	Low Q: High A: Low C: Low

The cobbles and pebbles in the biotope are likely to move as a result of penetration and/or sub surface disturbance. The characterizing and associated species would probably accrue damage from abrasion and scour and barnacles and littorinids trapped on the undersides of overturned pebbles would be unable to feed or respire. 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. This biotope is considered to have 'Low' resistance and 'High' resilience, to this pressure and sensitivity is therefore assessed as 'Low'.

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

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). This mixed substrata biotope occurs in estuaries in sheltered conditions where levels of suspended sediments are likely to be raised from riverine inputs and from re-suspension of sediments within the biotope. The level of suspended solids depends on a variety of factors including: substrate type, river flow, tidal height, water velocity, wind reach/speed and depth of water mixing (Parr *et al*. 1998). Transported sediment including silt and organic detritus can become trapped in the system where the river water meets seawater. Dissolved material in the river water flocculates when it comes into contact with the salt wedge pushing its way upriver. These processes result in elevated levels of suspended particulate material with peak levels confined to a discrete region (the turbidity maximum), usually in the upper-middle reaches, which moves up and down the estuary with the tidal ebb and flow.

A change in suspended solids at the pressure benchmark is likely to refer to changes on the UK TAG scale (2014) from intermediate (10-100 mg/l to medium turbidity (100-300 mg/l) or high turbidity (>300 mg/l). Increased suspended sediment may reduce growth rates in barnacles due to the energetic costs of cleaning sediment particles from feeding apparatus. *Elminius modestus* is more tolerant of turbidity than *Semibalanus balanoides* and may become the dominant barnacle. However, this will not alter the nature of the biotope. *Littorina littorea* is found in turbid estuaries where suspended sediment levels are high.

Sensitivity assessment. This biotope is not considered sensitive to decreased suspended sediments. An increase in suspended solids may increase the level of scour and deposition in this sheltered biotope and inhibit larval settlement. Increased suspended solids may reduce feeding rates of *Semibalanus balanoides*, although this may be compensated where the increased load of solids is due to organic matter inputs. Biotope resistance to an increase is assessed as 'Medium' and resilience as ‘High’ (following habitat recovery) so that the biotope is considered to have 'Low' sensitivity.

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

More direct evidence to assess this pressure was found for the characterizing species *Littorina littorea*, than *Semibalanus balanoides*. However, the lower limits of *Semibalanus balanoides* (as *Balanus balanoides*) appear to be set by levels of sand inundation on sand-affected rocky shores in New Hampshire (Daly & Mathieson, 1977), suggesting that this species is sensitive to the deposition of relatively coarse sediments, although whether this is due to repeated scour events removing juveniles rather than siltation effects (i.e. smothering, prevention of feeding) is not clear.

Littorina littorea through grazing and bulldozing actions may directly aid the removal of silts and sediments and remove the algal films that may accumulate silts (Bertness, 1984). On a protected New England rocky beach, Bertness (1984) showed how accumulation of sediments, due to the removal of the snail *Littorina littorea* changed the character of the habitat to one more typical of sedimentary habitats, with a decrease in the abundance of organisms characteristic of hard-bottom habitats, such as barnacles and encrusting algae (cited from Airoldi *et al*. 2003). Chandrasekara & Frid (1998) specifically tested the siltation tolerance of *Littorina littorea*. Burial to 5 cm caused mortality within 24 hours at simulated summer and winter temperatures if the snails could not crawl out of the sediment (Chandrasekara & Frid, 1998). If the sediment is well oxygenated and fluid (as with high water, high silt content) a few snails (1-6 out of 15 in the experiment, depending on temperature, sediment and water content) may be able to move back up through 5 cm of sediment (Chandrasekara & Frid, 1998). Approximately half of the test individuals could not regain the surface from 1 cm of burial except in the most favourable conditions (low temperatures, high water, high silt when a majority (10 out of 15) of the test cohort surfaced. Field observations support the findings that *Littorina littorea* are generally unable to survive smothering. Albrecht & Reise (1994) observed a population of *Littorina littorea* in a sandy bay near the Sylt island in the North Sea. They found that the accretion of mud within *Fucus* strands and subsequent covering of *Littorina* by the sediment resulted in them suffocating and a significant reduction in their abundance.

Sensitivity assessment. *Semibalanus balanoides* is found permanently attached to hard substrates and is a suspension feeder. This species, therefore, has no ability to escape from silty sediments which would bury individuals and prevent feeding and respiration. However, no direct evidence for sensitivity to siltation was found. Resistance to siltation is assessed as 'Low' for *Littorina littorea* based primarily on observations and experiments of Airoldi & Hawkins, (2007) and Chandrasekara & Frid, (1998), who demonstrated negative effects at deposit thicknesses at or far lower than the pressure benchmark. Within this sheltered biotope wave action or water flows are unlikely to rapidly mobilise and remove deposits alleviating the effect of smothering. Even small deposits of sediments are likely to result in local removal of littorinids. Biotope resistance is assessed as 'Low' based on the characterizing species. Resilience is assessed as 'High' and sensitivity is therefore considered to be 'Low'. Repeated deposition events, coupled with changes in water flow and wave action may lead to the establishment of *Ulva* spp. that trap sediments, this would significantly alter the character of the biotope.

Smothering and siltation rate changes (heavy)	None Q: High A: Medium C: High	High Q: High A: High C: High	Medium Q: High A: Medium C: High

More direct evidence to assess this pressure was found for the characterizing species *Littorina littorea*, than *Semibalanus balanoides*. However, the lower limits of *Semibalanus balanoides* (as *Balanus balanoides*) appear to be set by levels of sand inundation on sand-affected rocky shores in New Hampshire (Daly & Mathieson, 1977), suggesting that this species is sensitive to the deposition of relatively coarse sediments, although whether this is due to repeated scour events removing juveniles rather than siltation effects (i.e. smothering, prevention of feeding) is not clear.

The evidence for siltation effects on the characterizing species, *Littorina littorea* and *Patella vulgata* is outlined above for 'light' deposition. In summary, experiments by Chandrasekara & Frid, (1998) and Airoldi & Hawkins (2007) , supported by field observation, indicate that *Littorina littorea* would be unable to escape from sediment deposits of 30cm thickness and would rapidly die.

Sensitivity assessment. 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. *Semibalanus balanoides* is found permanently attached to hard substrates and is a suspension feeder. This species, therefore, has no ability to escape from silty sediments which would bury individuals and prevent feeding and respiration. Even small deposits of sediments are likely to result in local removal and death of littorinids. Resistance to siltation at the benchmark level is assessed as 'None' for *Littorina littorea* based primarily on the observations and experiments of Chandrasekara & Frid (1998), who demonstrated negative effects at deposit thicknesses far lower than the pressure benchmark. Within this sheltered biotope wave action or water flows are unlikely to rapidly mobilise and remove deposits alleviating the effect of smothering. Biotope resistance is assessed as 'None' based on the characterizing species. Resilience is assessed as 'High' and sensitivity is therefore considered to be 'Medium'.

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

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

Electromagnetic changes	No evidence (NEv) Q: NR A: NR C: NR	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. Wave action on exposed shores is likely to generate high levels of underwater noise. Other sources are not considered likely to result in effects on the biotope.

Introduction of light or shading	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 direct evidence to assess this pressure was found for the key characterizing species Patella vulgata and the littorinids. As both species occur on open rock and in crevices and under Fucus canopies they are considered tolerant of a range of light conditions. Semibalanus balanoides sheltered from the sun grew bigger than unshaded individuals (Hatton, 1938; cited in Wethey, 1984), although the effect may be due to indirect cooling effects rather than shading. Light levels have, however been demonstrated to influence a number of phases of the reproductive cycle in *Semibalanus balanoide*s. In general light inhibits aspects of the breeding cycle. Penis development is inhibited by light (Barnes & Stone, 1972) while Tighe-Ford (1967) showed that constant light inhibited gonad maturation and fertilization. Davenport & Crisp (unpublished data from Menai Bridge, Wales, cited from Davenport *et al*., 2005) found that experimental exposure to either constant darkness, or 6 h light: 18 h dark photoperiods induced autumn breeding in *Semibalanus*. They also confirmed that very low continuous light intensities (little more than starlight) inhibited breeding. Latitudinal variations in timing of the onset of reproductive phases (egg mass hardening) have been linked to the length of darkness (night) experienced by individuals rather than temperature (Davenport *et al*., 2005). Changes in light levels associated with climate change (increased cloud cover) were considered to have the potential to alter timing of reproduction (Davenport *et al*., 2005) and to shift the range limits of this species southward. However, it is not clear how these findings may reflect changes in light levels from artificial sources, and whether observable changes would occur at the population level as a result. There is, therefore, 'No evidence' on which to base an assessment.

Barrier to species movement	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 the key characterizing species *Patella vulgata*, *Semibalanus balanoides* and *Littorina littorea* are planktonic and are transported by water movements, barriers that reduce the degree of tidal excursion may alter larval supply 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. The associated macroalgae and *Littorina saxatilis* have either limited dispersal or produce crawl away juveniles rather than pelagic larvae (direct development). Barriers and changes in tidal excursion are not considered relevant to these species as dispersal is limited. As the key characterizing species 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) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant.

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	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

The characterizing species, *Semibalanus balanoides* and *Littorina littorea* and other common rocky shores species within the biotope, with the exception of *Mytilus edulis* which occurs in low densities, are not subject to translocation or cultivation. Commercial cultivation of *Mytilus edulis* involves the collection of juvenile mussel 'seed' or spat (newly settled juveniles ca 1-2cm 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 sensitivity assessments for *Mytilus edulis* bed biotopes). A review by Svåsand *et al*. (2007) concluded that there was a lack of evidence distinguishing between different *Mytilus edulis* populations to accurately assess the impacts of hybridisation with the congener *Mytilus galloprovincialis* 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.

Sensitivity assessment. No direct evidence was found regarding the potential for negative impacts of translocated mussel seed on wild *Mytilus edulis* populations. 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). Hybrids would 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 biotopes equally, as the main habitat forming species *Mytilus edulis* is translocated. Also, given the uncertainty in identification of the species, habitats or biotopes that are considered to be characterized by *Mytilus edulis* may in fact contain *Mytilus galloprovincialis*, their hybrids or a mosaic of the three. Presently, there is no evidence of impact resulting from genetic modification and translocation on *Mytilus edulis* beds in general or the clumps that characterize this biotope.

Introduction or spread of invasive non-indigenous species	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

This biotope is considered to be most vulnerable to invasive non-indigenous species that can out-compete the characterizing species and associated assemblage for space or those species that will predate on the characterizing species.

In terms of space occupation, the Australasian barnacle, *Austrominius modestus*, the Pacific oyster, *Magallana gigas* and the tunicates, *Botrylloides diegensis*, *Corella eumyota* may be most likely to occur in this 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 Asian shore crab has achieved high densities in mainland Europe (Sweet & Sewell, 2014). However, Brousseau & Goldberg (2007) found that even at high crab densitites the effects of predation on density of *Semibalanus balanoides* were limited as continued recruitment offset predation.

The Australasian barnacle *Austrominius* (previously *Elminius) modestus* was introduced to British waters on ships during the second world war. However, its overall effect on the dynamics of rocky shores has been small as *Austrominius modestus* has simply replaced some individuals of a group of co-occurring barnacles (Raffaelli & Hawkins, 1999). *Austrominius modestus* can tolerate lower salinities than the native barnacle *Semibalanus balanoides* (Gomes-Filho, *et al*., 2010) and may dominate this biotope, however this is not considered to lead to a significant change in biotope character or function.

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 and 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 *Crassostrea gigas*.

Although the results of studies of feeding preferences for *Sargassum muticum* over native macroalgae vary, *Littorina littorea* does feed on this species so shoreline colonization by this species would mean that food was still available (Withers *et al*. 1975). *Littorina littorea* also grazes on degraded or stressed *Didemnum vexillem* individuals (Valentine *et al*., 2007) and *Codium fragile* ssp. *tomentosoides* (Schiebling *et al*., 2008), so gains some benefit from the presence of these species. However, the mobility of the substratum, the variable salinity and the lack of tidepools may inhibit the colonization of this biotope by invasive, non-indigenous macroalgae.

A number of INIS that can settle and occupy hard substratum may threaten this biotope in the future if they become established. The tunicates *Didemnum vexillum* and *Asterocarpa humilis*, the hydroid *Schizoporella japonica* and the bryozoan *Watersipora subatra* (Bishop, 2012c; Bishop, 2015a; 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.

Sensitivity assessment. Overall, there is little evidence of this biotope being adversely affected by non-native species. Resistance Is therefore assessed as 'High' and recovery as 'High' (by default) so that the biotope is assessed as 'Not sensitive'. Changes in the identities, distribution or abundance of INIS may require this assessment to be updated.

Introduction of microbial pathogens	Medium Q: High A: Low C: Low	High Q: High A: Low C: Medium	Low Q: High A: Low C: Low

The characterizing species, littorinids and *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. 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 (Stefaniak *et al*., 2005).

Sensitivity assessment. Based on the characterizing species and the lack of evidence for widespread, high-levels of mortality due to microbial pathogens the biotope is considered to have 'High' resistance to this pressure and therefore 'High' resilience (by default), the biotope is therefore considered to be 'Not sensitive'.

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

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. The community structure within the biotope is likely to be altered but some individuals are likely to remain.

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).

Sensitivity assessment. In general collectors will be efficient at removing this species, resistance is therefore assessed as 'Low' (removal is not considered to be total as smaller individuals may escape), recovery is assessed as 'High' based on above evidence (Crossthwaite *et al*., 2012), so that 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. Intense harvesting of littorinids, would be likely to result in enhanced algal growth although the mobility of the boulders and cobbles may counteract the development of all but ephemeral, opportunistic algae.

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

Removal of the characterizing *littorinids* and barnacles would alter the character of the biotope. Removal of these species may result in the proliferation of ephemeral green algae, altering the classification of the biotope to the LR.FLR.Eph.Ulv biotope.

Sensitivity assessment. Removal of a large percentage of the characterizing species would alter the character of the biotope, so that it was bare rock. Resistance is therefore assessed as 'Low' and recovery as 'High', so that sensitivity is assessed as 'Low'.

Bibliography

Abou-Aisha, K.M., Kobbia, I., El Abyad, M., Shabana, E.F. & Schanz, F., 1995. Impact of phosphorus loadings on macro-algal communities in the Red Sea coast of Egypt. *Water, Air, and Soil Pollution*, **83** (3-4), 285-297.

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

Albrecht, A. & Reise, K., 1994. Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. *Helgoländer Meeresuntersuchungen*, **48** (2-3), 243-256.

Albrecht, A.S., 1998. Soft bottom versus hard rock: Community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **229** (1), 85-109.

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., 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.

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.

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

Barnes, H., 1956. *Balanus balanoides* (L.) in the Firth of Clyde: the development and annual variation in the larval population and the causative factors. *Journal of Animal Ecology*, **25**, 72-84.

Barnes, H. & Stone, R., 1972. Suppression of penis development in *Balanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology*, **9 (**3), 303-309.

Barnes, H., 1953. The effect of lowered salinity on some barnacle nauplii. *Journal of Animal Ecology*, **22**, 328-330.

Barnes, H., 1957. Processes of restoration and synchronization in marine ecology. The spring diatom increase and the 'spawning' of the common barnacle *Balanus balanoides* (L.). *Année Biologique. Paris*, **33**, 68-85.

Barnes, H., 1963. Light, temperature and the breeding of *Balanus balanoides*. *Journal of the Marine Biological Association of the United Kingdom*, **43** (03), 717-727.

Barnes, 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.

Bauer, B., Fioroni, P., Ide, I., Liebe, S., Oehlmann, J., Stroben, E. & Watermann, B., 1995. TBT effects on the female genital system of *Littorina littorea*: a possible indicator of tributyl tin pollution. *Hydrobiologia*, **309**, 15-27.

Baxter, J.M., 1984. The incidence of *Polydora ciliata* and *Cliona celata* boring the shell of *Patella vulgata* in Orkney. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 728-729.

Bayne, B.L., 1976a. The biology of mussel larvae. In *Marine mussels: their ecology and physiology* (ed. B.L. Bayne), pp. 81-120. Cambridge: Cambridge University Press. [International Biological Programme 10.]

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

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

Berthe, F.C.J., Le Roux, F., Adlard, R.D. & Figueras, A., 2004. Marteiliosis in molluscs: a review. *Aquatic Living Resources*, **17** (4), 433-448.

Bertness, M.D., 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology*, **65**, 370-381.

Bertness, M.D., Gaines, S. D., Stephens, E. G., & Yund, P. O. , 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, **156** (2), 199-215.

Bertness, M.D., Gaines, S.D., Bermudez, D. & Sanford, E., 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*, 75, 91-100.

Bertocci, I., Araujo, R., Vaselli, S. & Sousa-Pinto, I., 2011. Marginal populations under pressure: spatial and temporal heterogeneity of *Ascophyllum nodosum* and associated assemblages affected by human trampling in Portugal. Marine Ecology Progress Series, **439**, 73-82.

Bishop, J. 2012c. Carpet Sea-squirt, *Didemnum vexillum.Great Britain Non-native Species Secretariat* [On-line]. [cited 30/10/2018]. Available from: http://www.nonnativespecies.org/factsheet/factsheet.cfm?speciesId=1209

Bishop, J. 2011a. *Botrylloides cf. diegensis*. *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

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

Blackmore, D.T., 1969. Growth, reproduction and zonation of *Patella vulgata*. *Journal of Experimental Marine Biology and Ecology*, **3**, 200-213.

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.

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. & McGladdery, S.E., 1996. Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish. SeaLane 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., 1985. The biology of the limpet *Patella vulgata* L. in the British Isles: spawning time as a factor determining recruitment sucess. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.*, (ed. P.G. Moore & R. Seed), Hodder and Stoughton, London, pages 178-193.

Bowman, R.S. and Lewis, J.R., 1986. Geographical variation in the breeding cycles and recruitment of *Patella* spp. *Hydrobiologia*, **142**, 41-56.

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., 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.]

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.

Brouardel, J., 1948. Etude du mode d'infestation des Patelles par *Urceolaria patellae* (Cuenot): influence de l'espece de Patelle. *Bulletin du Laboratoire maritime de Dinard*, **30**, 1-6.

Brousseau, D.J. & Goldberg, R., 2007. Effect of predation by the invasive crab *Hemigrapsus sanguineus* on recruiting barnacles *Semibalanus balanoides* in western Long Island Sound, USA. *Marine Ecology Progress Series*, **339**, 221-228.

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.

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., 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.

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

Buschbaum, C., Buschbaum, G., Schrey, I. & Thieltges, D., 2007. Shell boring polychaetes affect gastropod shell strength and crab predation. *Marine Ecology Progress Series*, **329**, 123-130.

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.

Casey, J.D., De Grave, S. & Burnell, G.M., 1998. Intersex and *Littorina littorea* in Cork Harbour: results of a medium-term monitoring programme. *Hydrobiologia*, **378**, 193-197.

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.

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/

Connell, J.H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs*, **31**, 61-104.

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

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

Crisp, D., 1961. Territorial behaviour in barnacle settlement. *Journal of Experimental Biology*, **38** (2), 429-446.

Crisp, D. & Patel, B., 1969. Environmental control of the breeding of three boreo-arctic cirripedes. *Marine Biology*, **2** (3), 283-295.

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

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

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, PJ 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.

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.

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., Berggren, M.S., Brattegard, T., Brattenborg, N., Burrows, M., Jenkins, S., McGrath, D., MacNamara, R., Sneli, J.-A. & Walker, G., 2005. Doses of darkness control latitudinal differences in breeding date in the barnacle *Semibalanus balanoides*. *Journal of the Marine Biological Association of the United Kingdom*, **85** (01), 59-63.

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 Vooys, C.G.N., 1987. Elimination of sand in the blue mussel *Mytilus edulis*. *Netherlands Journal of Sea Research*, **21**, 75-78.

Deutsch, U. & Fioroni, P., 1996. Effects of tributyltin (TBT) and testosterone on the female genital system in the mesogastropod *Littorina littorea* (Prosobranchia). *Helgolander Meeresuntersuchungen*, **50**, 105-115.

Diaz, E.R., Kraufvelin, P. & Erlandsson, J., 2012. Combining gut fluorescence technique and spatial analysis to determine *Littorina littorea* grazing dynamics in nutrient-enriched and nutrient-unenriched littoral mesocosms. *Marine Biology*, **159** (4), 837-852.

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., 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.

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.

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.

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.

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.

Erlandsson, J. & Johannesson, K., 1992. Sexual selection on female size in a marine snail, *Littorina littorea*. *Journal of Experimental Marine Biology and Ecology*, **181**, 145-157.

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.

Feare, C.J., 1970b. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus*. *Oecologia*, **5**, 1-18.

Fish, J. D., 1972. The breeding cycle and growth of open coast and estuarine populations of *Littorina littorea*. *Journal of the Marine Biological Association of the United Kingdom*, **52**, 1011-1019.

Fletcher, H. & Frid, C.L.J., 1996a. Impact and management of visitor pressure on rocky intertidal algal communities. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **6**, 287-297.

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.

Foster, P., Hunt, D.T.E. & Morris, A.W., 1978. Metals in an acid mine stream and estuary. *Science of the Total Environment*, **9**, 75-86.

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.

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

Gallagher, M.C., Davenport, J., Gregory, S., McAllen, R. & O'Riordan, R., 2015. The invasive barnacle species, *Austrominius modestus*: Its status and competition with indigenous barnacles on the Isle of Cumbrae, Scotland. *Estuarine, Coastal and Shelf Science*, **152**, 134-141.

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.

Gomes-Filho, J., Hawkins, S., Aquino-Souza, R. & Thompson, R., 2010. Distribution of barnacles and dominance of the introduced species *Elminius modestus* along two estuaries in South-West England. *Marine Biodiversity Records*, **3**, e58.

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, 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.

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.

Gyory, J. & Pineda, J., 2011. High-frequency observations of early-stage larval abundance: do storms trigger synchronous larval release in *Semibalanus balanoides*? *Marine Biology*, **158** (7), 1581-1589.

Gyory, J., Pineda, J. & Solow, A., 2013. Turbidity triggers larval release by the intertidal barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*, **476**, 141-151.

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

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

Hawkins, S.J. & Hartnoll, R.G., 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.

Hawkins, S.J., 1981. The influence of *Patella* grazing on the fucoid/barnacle mosaic on moderately exposed rocky shores. *Kieler Meeresforschungen*, **5**, 537-543.

Hawkins, S.J., Hartnoll, R.G., Kain, J.M. & Norton, T.A., 1992. Plant-animal interactions on hard substrata in the north-east Atlantic. In *Plant-animal interactions in the marine benthos* (ed. D.M. John, S.J. Hawkins & J.H. Price), pp. 1-32. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]

Hawkins, S.J., Proud, S.V., Spence, S.K. & Southward, A.J., 1994. From the individual to the community and beyond: water quality, stress indicators and key species in coastal systems. In *Water quality and stress indicators in marine and freshwater ecosystems: linking levels of organisation (individuals, populations, communities)* (ed. D.W. Sutcliffe), 35-62. Ambleside, UK: Freshwater Biological Association.

Hawkins, S.J., Southward, A.J. & Barrett, R.L., 1983. Population structure of *Patella vulgata* (L.) during succession on rocky shores in southwest England. *Oceanologica Acta*, Special Volume, 103-107.

Highsmith, R.C., Rucker, T.L., Stekoll, M.S., Saupe, S.M., Lindeberg, M.R., Jenne, R.N. & Erickson, W.P., 1996. Impact of the *Exxon Valdez* oil spill on intertidal biota. In *Proceedings of the* Exxon Valdez *Oil Spill Symposium. American Fisheries Society Symposium*, no. 18, *Anchorage, Alaska, USA, 2-5 February 1993,* (ed. S.D. Rice, R.B. Spies, D.A., Wolfe & B.A. Wright), pp.212-237.

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

Hills, J. & Thomason, J., 1998. The effect of scales of surface roughness on the settlement of barnacle (*Semibalanus balanoides*) cyprids. *Biofouling*, **12** (1-3), 57-69.

Hily, C., Potin, P. & Floch, J.Y. 1992. Structure of subtidal algal assemblages on soft-bottom sediments - fauna flora interactions and role of disturbances in the Bay of Brest, France. *Marine Ecology Progress Series*, **85**, 115-130.

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.

Houghton, J.P., Lees, D.C., Driskell, W.B., Lindstrom & Mearns, A.J., 1996. Recovery of Prince William Sound intertidal epibiota from *Exxon Valdez* oiling and shoreline treatments, 1989 through 1992. In *Proceedings of the* Exxon Valdez *Oil Spill Symposium. American Fisheries Society Symposium*, no. 18, *Anchorage, Alaska, USA, 2-5 February 1993,* (ed. S.D. Rice, R.B. Spies, D.A., Wolfe & B.A. Wright), pp.379-411.

Janke, K., 1990. Biological interactions are their role in the community structure in the rocky intertidal of Helgoland (German Bight, North Sea) *Helgolander Wissenschaftliche Meeresuntersuchungen*, **44**, 219-263.

Jenkins, S., Åberg, P., Cervin, G., Coleman, R., Delany, J., Della Santina, P., Hawkins, S., LaCroix, E., Myers, A. & Lindegarth, M., 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.)(Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*, **243** (2), 209-225.

Jenkins, S., Aberg, P., Cervin, G., Coleman, R., Delany, J., Hawkins, S., Hyder, K., Myers, A., Paula, J. & Power, A., 2001. Population dynamics of the intertidal barnacle *Semibalanus balanoides* at three European locations: spatial scales of variability. *Marine Ecology Progress Series*, **217**, 207-217.

Jenkins, S.R., Norton, T.A. & Hawkins, S.J., 1999. Settlement and post-settlement interactions between *Semibalanus balanoides* (L.)(Crustacea: Cirripedia) and three species of fucoid canopy algae. *Journal of Experimental Marine Biology and Ecology*, **236** (1), 49-67.

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

Jørgensen, C.B., 1981. Mortality, growth, and grazing impact on a cohort of bivalve larvae, *Mytilus edulis* L. *Ophelia*, **20**, 185-192.

Jørgensen, T., 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *ICES Journal du Conseil*, **46**, 235-248.

Kaiser, M.J. & Spencer, B.E., 1994. Fish scavenging behaviour in recently trawled areas. *Marine Ecology Progress Series*, **112** (1-2), 41-49.

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.

Kendall, M.A., Bowman, R.S., Williamson, P. & Lewis, J.R., 1985. Annual variation in the recruitment of *Semibalanus balanoides* on the North Yorkshire coast 1969-1981. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 1009-1030.

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

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

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 Ecolog*y, **364** (1), 1-10.

Landes, A. & Zimmer, M., 2012. Acidification and warming affect both a calcifying predator and prey, but not their interaction. *Marine Ecology Progress Series*, **450**, 1-10.

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

Langston, W.J. & Zhou Mingjiang, 1986. Evaluation of the significance of metal-binding proteins in the gastropod *Littorina littorea*. *Marine Biology*, **92**, 505-515.

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.

Le Quesne W.J.F. 2005. *The response of a protandrous species to exploitation, and the implications for management: a case study with patellid limpets.* PhD thesis. University of Southampton, Southampton, United Kingdom.

Lewis, J. & Bowman, R.S., 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, **17** (2), 165-203.

Lewis, J.R., 1964. *The Ecology of Rocky Shores.* London: English Universities Press.

Little, C. & Kitching, J.A., 1996. *The Biology of Rocky Shores.* Oxford: Oxford University Press.

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.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.

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, 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

Loosanoff, V.L., 1962. Effects of turbidity on some larval and adult bivalves. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **14,** 80-95.

Lubchenco, J., 1983. *Littornia* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology*, **64** (5), 1116-1123.

Lubchenco, J., 1978. Plant species diversity in a marine intertidal community, importance of herbivore food preference and algal competitive abilities. *American Naturalist*, **112**, 23-39.

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.

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

Markert, A., Wehrmann, A. & Kröncke, 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.

Marshall, D.J. & McQuaid, C.D., 1993. Effects of hypoxia and hyposalinity on the heart beat of the intertidal limpets *Patella granvlaris* (Prosobranchia) and *Siphonaria capensis* (Pulmonata). *Comparative Biochemistry and Physiology Part A: Physiology*, **106** (1), 65-68

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.

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.

Mieszkowska, N., Burrows, M.T., Pannacciulli, F.G. & Hawkins, S.J., 2014. Multidecadal signals within co-occurring intertidal barnacles *Semibalanus balanoides* and *Chthamalus* spp. linked to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems*, **133**, 70-76.

Monterosso, B., 1930. Studi cirripedologici. VI. Sul comportamento di *Chthamalus stellatus* in diverse condizioni sperimentali. Atti Accad. Naz. Lincei Rc., **9**, 501-504.

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.

Mouritsen, K. N., Gorbusin, A. & Jensen, K. T., 1999. Influence of trematode infections on in situ growth rates of *Littorina littorea*. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 425-430.

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.

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

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

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.

Oehlmann, J., Bauer, B., Minchin, D., Schulte-Oehlmann, U., Fioroni, P. & Markert, B., 1998. Imposex in *Nucella lapillus* and intersex in *Littorina littorea*: interspecific comparison of two TBT- induced effects and their geographical uniformity. *Hydrobiologia*, **378**, 199-213

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.

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

Petraitis, P.S., Rhile, E.C. & Dudgeon, S., 2003. Survivorship of juvenile barnacles and mussels: spatial dependence and the origin of alternative communities. *Journal of Experimental Marine Biology and Ecology*, **293** (2), 217-236.

Pieters, H., Klutymans, J.H., Zandee, D.I. & Cadee, G.C., 1980. Tissue composition and reproduction of *Mytilus edulis* dependent upon food availability. *Netherlands Journal of Sea Research*, **14**, 349-361.

Povey, A. & Keough, M.J., 1991. Effects of trampling on plant and animal populations on rocky shores. *Oikos*, **61**: 355-368.

Prendergast, G.S., Zurn, C.M., Bers, A.V., Head, R.M., Hansson, L.J. & Thomason, J.C., 2009. The relative magnitude of the effects of biological and physical settlement cues for cypris larvae of the acorn barnacle, *Semibalanus balanoides* L. *Biofouling*, **25** (1), 35-44.

Purchon, R.D., 1937. Studies on the biology of the Bristol Channel. *Proceedings of the Bristol Naturalists' Society*, **8**, 311-329.

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.

Rainbow, P.S., 1984. An introduction to the biology of British littoral barnacles. *Field Studies*, **6**, 1-51.

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.

Read, K.R.H. & Cumming, K.B., 1967. Thermal tolerance of the bivalve mollusc *Modiolus modiolus* (L.), *Mytilus edulis* (L.) and *Brachiodontes demissus* (Dillwyn). *Comparative Biochemistry and Physiology*, **22**, 149-155.

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.

Robles, C., 1982. Disturbance and predation in an assemblage of herbivorous *Diptera* and algae on rocky shores. *Oecologia*, **54** (1), 23-31.

Rognstad, R.L., Wethey, D.S. & Hilbish, T.J., 2014. Connectivity and population repatriation: limitations of climate and input into the larval pool. *Marine Ecology Progress Series*, **495**, 175-183.

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.

Scheibling, R.E., Lyons, D.A. & Sumi, C.B., 2008. Grazing of the invasive alga *Codium fragile* ssp. *tomentosoides* by the common periwinkle *Littorina littorea*: effects of thallus size, age and condition. *Journal of Experimental Marine Biology and Ecology*, **355** (2), 103-113.

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.

Seapy , R.R. & Littler, M.M., 1982. Population and Species Diversity Fluctuations in a Rocky Intertidal Community Relative to Severe Aerial Exposure and Sediment Burial. *Marine Biology*, **71**, 87-96.

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., 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.

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]

Smith, B.S., 1980. The estuarine mud snail, *Nassarius obsoletus*: abnormalities in the reproductive system. *Journal of Molluscan Studies*, **46**, 247-256.

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

Southward, A.J. & Crisp, D.J., 1956. Fluctuations in the distribution and abundance of intertidal barnacles. *Journal of the Marine Biological Association of the United Kingdom*, **35**, 211-229.

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., 1964. Limpet grazing and the control of vegetation on rocky shores. In *Grazing in Terrestrial and Marine Environments, British Ecological Society Symposium* No. 4 (ed. D.J. Crisp), 265-273.

Southward, A.J., Hawkins, S.J. & Burrows, M.T., 1995. Seventy years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, **20**, 127-155.

Stefaniak, L.M., McAtee, J. & Shulman, M.J., 2005. The costs of being bored: Effects of a clionid sponge on the gastropod *Littorina littorea* (L). *Journal of Experimental Marine Biology and Ecology*, **327** (1), 103-114.

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.

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. & Sewell, J. 2014. Asian shore crab, *Hemigrapsus sanguineus*. *Great Britain Non-native Species Secretariat*. [cited 16/06/2015]. Available from: <http://www.nonnativespecies.org

Terry, L. & Sell, D., 1986. Rocky shores in the Moray Firth. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences*, **91**, 169-191.

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., Richardson, C., Seed R. & Walker G., 2000. Quantification of mussel (*Mytilus edulis*) growth from power station cooling waters in response to chlorination procedures. *Biofouling*, **16**(1), 1-15.

Thompson, R.C., Olsen, Y., Mitchell, R.P., Davis, A., Rowland, S.J., John, A.W., McGonigle, D. & Russell, A.E., 2004. Lost at sea: where is all the plastic? *Science*, **304** (5672), 838-838.

Tighe-Ford, D., 1967. Possible mechanism for the endocrine control of breeding in a cirripede. *Nature*, **216**, 920-921.

Trager, G. C., Hwang, J. S., & Strickler, J. R. 1990. Barnacle suspension-feeding in variable flow. *Marine Biology*, **105**(1), 117-127.

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

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.

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.

Wethey, D.S., 1985. Catastrophe, Extinction, and Species Diversity: A Rocky Intertidal Example. *Ecology*, **66** (2), 445-456.

Wethey, D.S., 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. *The Biological Bulletin*, **167** (1), 176-185.

Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P. & Brannock, P.M., 2011. Response of intertidal populations to climate: effects of extreme events versus long term change. *Journal of Experimental Marine Biology and Ecology*, **400** (1), 132-144.

Whitehouse, J., Coughlan, J., Lewis, B., Travade, F. & Britain, G., 1985. The control of biofouling in marine and estuarine power stations: a collaborative research working group report for use by station designers and station managers. *Central Electricity Generating Board*

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., 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.

Withers, R., Farnham, W., Lewey, S., Jephson, N., Haythorn, J. & Gray, P., 1975. The epibionts of *Sargassum muticum* in British waters. *Marine Biology*, **31** (1), 79-86.

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.