



MarLIN

Marine Information Network

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

Semibalanus balanoides, *Patella vulgata* and *Littorina* spp. on exposed to moderately exposed or vertical sheltered eulittoral rock

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

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2018-09-07

A report from:

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

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This review can be cited as:

Tillin, H.M. & Hill, J.M., 2018. [*Semibalanus balanoides*], [*Patella vulgata*] and [*Littorina*] spp. on exposed to moderately exposed or vertical sheltered eulittoral rock. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom.
DOI <https://dx.doi.org/10.17031/marlinhab.40.1>



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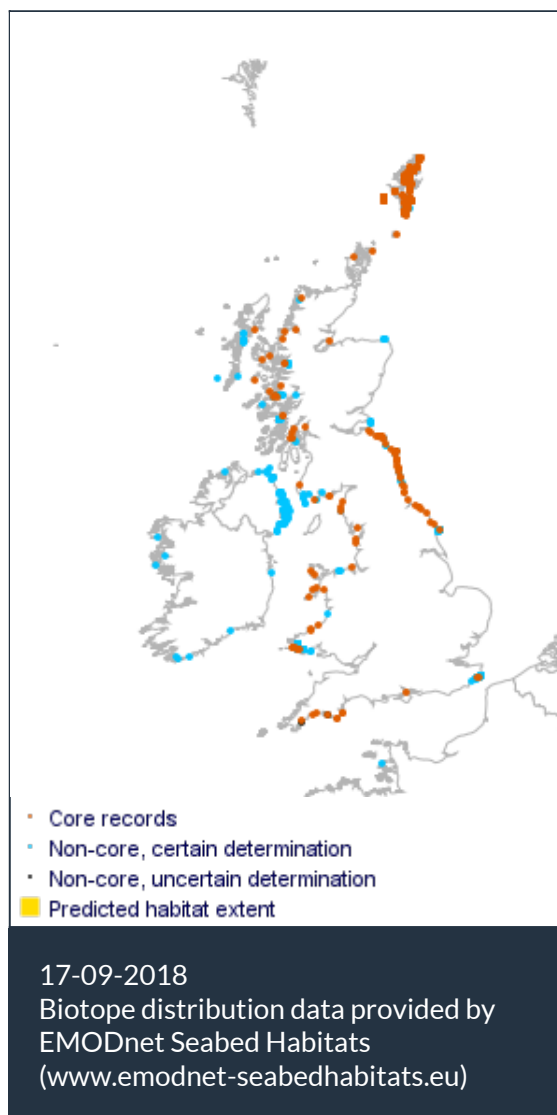
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Semibalanus balanoides, *Patella vulgata* and *Littorina* spp. on exposed to moderately exposed or vertical sheltered eulittoral rock

Photographer: Eleanor Murray

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Researched by Dr Heidi Tillin & Jacqueline Hill

Referred by This information is not refereed.

Summary

☰ UK and Ireland classification

EUNIS 2008 A1.1131

Semibalanus balanoides, *Patella vulgata* and *Littorina* spp. on exposed to moderately exposed or vertical sheltered eulittoral rock

JNCC 2015 LR.HLR.MusB.Sem.Sem

Semibalanus balanoides, *Patella vulgata* and *Littorina* spp. on exposed to moderately exposed or vertical sheltered eulittoral rock

JNCC 2004 LR.HLR.MusB.Sem.Sem

Semibalanus balanoides, *Patella vulgata* and *Littorina* spp. on exposed to moderately exposed or vertical sheltered eulittoral rock

1997 Biotope LR.ELR.MB.BPat.Sem

Semibalanus balanoides on exposed or moderately exposed, or vertical sheltered, eulittoral rock

🔍 Description

Very exposed to sheltered mid to upper eulittoral bedrock and large boulders characterised by dense barnacles *Semibalanus balanoides* and the limpet *Patella vulgata*. The community has a relatively low diversity of species though occasional cracks and crevices in the rock can provide a refuge for small individuals of the mussel *Mytilus edulis*, the winkle *Littorina* spp. and the whelk *Nucella lapillus*. Seaweeds are usually not found in high numbers though fissures and crevices in the bedrock can hold a sparse algae community, though patches of the red seaweed *Osmundea pinnatifida* can be present throughout the zone. On some shores the olive green lichen *Verrucaria mucosa* can be present in some abundance (Frequent). Records should not be assigned to this species impoverished biotope if there is a significant number or abundance of seaweeds.

On very exposed to exposed shores *Chthamalus* spp. (see Cht.Cht) often forms a distinct white band above a darker band of *Semibalanus balanoides* in the mid eulittoral zone. Alternatively, found above Sem are the black lichen *Verrucaria maura* dominated biotopes (Ver.Ver or Ver.B). In the lower eulittoral and the sublittoral fringe is a community dominated by the wrack *Himanthalia elongata* and various red seaweeds including *Corallina officinalis*, *Mastocarpus stellatus* and *Osmundea pinnatifida* (Him; Coff; Osm) or the mussel and barnacle dominated biotope MytB. Sem.Sem may occur on steep and vertical faces on more sheltered shores, while fucoids dominate the flatter areas (Sem.FvesR; FvesB). Periods with little scour or less severe storms can allow a seaweed community to develop creating a more diverse biotope (i.e. Fves). This is a dynamic process, which will change individual sites over time. More information is required to validate this hypothesis. (Information from Connor *et al.*, 2004; JNCC, 2015).

↓ Depth range

Upper shore, Mid shore

🏛️ Additional information

-

✓ Listed By

- none -

🔗 Further information sources

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Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

The biotope description and information on the associated species are all taken from Connor *et al.* (2004) unless referenced otherwise. The key characterizing species for this biotope, on which the sensitivity assessments are based, are the barnacle *Semibalanus balanoides* and the limpet *Patella vulgata*. *Patella vulgata* is considered a key structuring species for this biotope, as its grazing controls the establishment of other species on the rock surface. *Patella vulgata* grazing can control the character of the shore by grazing algae and newly settled barnacle larvae. Even a small, localised temporary absence of limpets (Southward, 1964; Hawkins, 1981; Hawkins *et al.*, 1983) can alter the biological assemblage. Significant limpet kills resulting from the widespread use of dispersants after the *Torrey Canyon* oil spill dramatically altered rocky shore communities. *Laminaria digitata*, for example, was able to extend 2 m up the shore in the absence of limpets and there were dense growths of ephemeral green seaweeds followed by equally dense growth of furoids (Southward & Southward, 1978; Hawkins & Southward, 1992). The hard rock substratum and exposure to wave action are key environmental factors structuring this biotope and are therefore considered, where relevant, in the sensitivity assessments.

The biotope has a relatively low diversity of associated species; cracks and crevices in the rock can provide a refuge for small individuals of the mussel *Mytilus edulis*, the winkle *Littorina saxatilis* and the whelk *Nucella lapillus*. Seaweeds are usually not found in high numbers although fissures and crevices in the bedrock can hold a sparse algal community including the green seaweed *Ulva intestinalis*. On some shores, the olive green lichen *Verrucaria mucosa* can be present in some abundance. As these species occur in low numbers and are characteristic of many types of rocky shores they are not considered to be of specific importance to this biotope. On some shores, particularly those which are moderately exposed to wave action, temporal fluctuations in the abundance of limpets, barnacles and furoid seaweeds may occur controlled by the interplay of environmental factors such as storm events and biological factors such as grazing. As a result, over a number of years, a single shore may cycle between the barnacle-*Patella vulgata* dominated biotope and a *Fucus vesiculosus*-dominated biotope.

Resilience and recovery rates of habitat

Recovery of the attached characterizing species, *Semibalanus balanoides* and the algal turfs will depend on recolonization by larvae. *Patella vulgata* is mobile, but the ability to relocate depends on the shore type and roughness (as described below). Most of the characterizing animal species, such as *Mytilus edulis*, produce pelagic larvae. As these are common, widespread species, where the footprint of the impact is relatively small, larval supply from adjacent populations should support recolonization. Where source populations are very distant due to regional impacts or habitat discontinuities, larval supply and recovery could be affected. Changes and recovery trajectories following the removal of key species are unpredictable and interactions between the key species may be positive or negative. Limpets and littorinids may enhance barnacle settlement by grazing and removing algae (Hawkins, 1983) or by depositing pedal mucus trails that attract barnacle larvae (Holmes *et al.*, 2005). Barnacles and small clumps of *Mytilus edulis* may enhance survival of small limpets by moderating environmental stresses but they may also have negative effects on recruitment by occupying space and by limiting access to grazing areas (Lewis & Bowman (1975). Dense coverings of mussels and furoids, however, inhibit settlement of larvae through competition for space or prevention of settlement (Lewis & Bowman, 1975). Limpets may also crush and displace newly settled individuals (Safriel *et al.*, 1994). Barnacles may enhance survival

of small limpets by moderating environmental stresses but they may also have negative effects on recruitment by occupying space and by limiting access to grazing areas. On the wave exposed shores that this biotope occurs on, grazing may limit initial settlement of macroalgae but wave action will limit the presence of adults and larger species through, breakage and drag effects leading to loss. Mrowicki *et al.*, (2014) found that limpet and barnacle removal allowed ephemeral and furoid macroalgae to establish on sheltered and wave exposed shores in Ireland. Unlike the animal species macroalgae have short dispersal distances, over tens of metres (Dudgeon *et al.*, 2001) and therefore recovery will require the presence of adults.

Recovery rates. Recolonization of *Patella vulgata* on rocky shores is rapid as seen by the appearance of limpet spat six months after the *Torrey Canyon* oil spill reaching peak numbers 4-5 years after the spill. Similarly, following the creation of a new rocky shore in the Moray Firth, *Patella vulgata* was present in quadrats after 3 years (Terry & Sell, 1986). However, although recolonization was rapid on the oil-impacted shores, the alteration to the population structure (size and age class) persisted for about 15 years because of the complex cycles of dominance (see below) involving limpets, barnacles and algae (Hawkins & Southward, 1992; Lewis & Bowman, 1975). Hence the establishment of furoids if *Patella vulgata* and other grazers were absent may lead to the longer-term exclusion of this species.

On rocky shores, 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 the 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).

Life histories and reproduction. In northern England, limpets reached sexual maturity in their second year (Blackmore, 1969) and thereafter reproduced annually. Limpets may change sex during their lifetime, with younger animals being male and older animals tending to be female (Blackmore, 1969). In Robin Hood's Bay, Lewis & Bowman (1975) observed spawning of *Patella vulgata* in the Autumn, with spatfall occurring in winter when desiccation pressures were lower.

The rate and density of colonization are affected by the presence of other species. Lewis & Bowman (working in Robin Hood's Bay in northern England) observed that mussels promote settlement of *Patella vulgata*. The settlement was also higher amongst barnacles and light coverings of algae. Dense coverings of mussels and furoids, however, inhibit settlement through competition for space or prevention of settlement.

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

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

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

Resilience assessment. No evidence for recovery rates was found specifically for this biotope. The evidence suggests that the size of the footprint of an impact and the magnitude will influence the recovery rates by mediating settlement and post-settlement recruitment. Barnacles are attracted to settle in the presence of adults of the same species (Prendergast *et al.*, 2009; so that the presence of adults will facilitate recovery. Resilience is assessed as '**High**' (within 2 years) where resistance is 'High' (no significant impact) or 'Medium' (<25% of characteristic biotope removed). A resistance of 'Medium' assumes that either a large proportion of the biotope is unimpacted or that the entire biotope is impacted but only a proportion of the characterizing species are removed, with unimpacted areas or individuals supporting recovery. Resilience is assessed as '**Medium**' (2-10 years) where resilience is 'None' or 'Low' as recruitment may be episodic and the age structure of the limpet population will require more time to recover.

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

Hydrological Pressures

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

At Great Cumbrae, the median upper lethal temperature limit in laboratory tests on *Semibalanus balanoides* was approximately 35°C (Davenport & Davenport, 2005). 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 by impacting the success of reproduction phases. The distribution of both the key characterizing species, *Semibalanus balanoides* and *Patella vulgata* are 'northern' with their range extending from Portugal or Northern Spain to the Arctic circle. Populations in the southern part of England are therefore relatively close to the southern edge of their geographic range.

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 rather than *Semibalanus balanoides* (Southward *et al.*, 1995). *Chthamalus montagui* and *Chthamalus stellatus* are warm water species, with a northern limit of distribution in Britain so are likely to be tolerant of long-term increases in temperature. Similarly, the limpet *Patella depressa* is a southern species and is therefore considered more tolerant of increased temperature. Thus, an increase in temperature over longer timescales could lead to a change in the dominant species of barnacle and limpet, particularly in more southern regions.

The body temperature of *Patella vulgata* can exceed 36°C in the field, (Davies, 1970), adults become non-responsive at 37-38°C and die at temperatures of 42°C (Evans, 1948). Lower temperatures enhance feeding rates in adults (Thompson *et al.*, 2004). Juvenile tolerance of warm air temperatures and desiccation may be lower than adults. Juveniles require damp areas of rock (Lewis & Bowmna, 1975) and the bare rock surfaces typical of this biotope, present a harsher habitat than the associated crevices and cracks. Long-term time studies in southern England suggest that *Patella vulgata* has become scarcer following warmer summers, while *Patella depressa* increase in abundance (Southward *et al.*, 1995). Increased temperatures may alter spawning cues and reproduction success in *Patella vulgata* populations. Observations suggest that spawning is initiated in autumn storms with greater wave action when seawater temperatures drop below 12°C (Bowman 1985; Bowman & Lewis, 1986; LeQuesne, 2005). In northern Portugal, warming seas appear to be linked to a shortening of the reproductive period and the lack of multiple spawning events in *Patella vulgata* and other northern species (Ribeiro *et al.*, 2009).

Most of the other species within the biotope are eurythermal (e.g. *Nucella lapillus* and *Mytilus edulis*) and are hardy intertidal species that tolerate long periods of exposure to the air and consequently wide variations in temperature (Davenport & Davenport, 2005). In addition, most species are distributed to the north and south of the British Isles and unlikely to be adversely affected by long-term temperature changes at the benchmark level. *Corallina officinalis*, however, experienced

severe damage during the unusually hot summer of 1983 (Hawkins & Hartnoll, 1985).

Sensitivity assessment. Adult *Semibalanus balanoides* and *Patella vulgata* are considered likely to be able to tolerate an acute or chronic change, however, if an acute change in temperature occurred in autumn or winter it could disrupt reproduction, 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 (Wetthey *et al.*, 2011, Rognstad *et al.*, 2014). Similarly, *Patella vulgata* is common, widespread species and therefore larvae are likely to be supplied by local populations to counteract local reproductive failures. Resistance 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: Medium C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium 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* was -16.4°C .

The distribution of both the key characterizing species, *Semibalanus balanoides* and *Patella vulgata* are 'northern' with their range extending from Portugal or northern Spain 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). The barnacle *Semibalanus balanoides* is primarily a 'northern' species with an arctic-boreal distribution. 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). A decrease in temperature at the pressure benchmark is therefore unlikely to negatively affect this species. The limpet, *Patella vulgata* can also tolerate long periods of exposure to the air and consequently wide variations in temperature. Adults are also largely unaffected by short periods of extreme cold. Ekaratne & Crisp (1984) found adult limpets continuing to grow over winter when temperatures fell to -6°C and stopped only by still more severe weather. However, loss of adhesion after exposure to -13°C has been observed

with limpets falling off rocks and therefore becoming easy prey to crabs or birds (Fretter & Graham, 1994). However, in the very cold winter of 1962-3 when temperatures repeatedly fell below 0°C over a period of two months large numbers of *Patella vulgata* were found dead (Crisp, 1964). Periods of frost may also kill juvenile *Patella vulgata*, resulting in recruitment failures in some years (Bowman & Lewis, 1977).

The associated species *Mytilus edulis* is a eurytopic species found in a wide temperature range and in areas which frequently experience freezing conditions and are vulnerable to ice scour (Seed & Suchanek 1992). After acclimation of individuals of *Mytilus edulis* to 18°C, Kittner & Riisgaard (2005) observed that the filtrations rates were at their maximum between 8.3 and 20°C and below this at 6°C the mussels closed their valves. However, after being acclimated at 11°C for five days, the mussels maintained the high filtration rates down to 4°C. Hence, given time, mussels can acclimatise and shift their temperature tolerance. Filtration in *Mytilus edulis* was observed to continue down to -1°C, with high absorption efficiencies (53-81%) (Loo, 1992).

Sensitivity assessment. Based on the wide temperature tolerance range of *Patella vulgata* 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. Based on the characterizing species and *Mytilus edulis* this biotope is considered to have a 'High' resistance and 'High' resilience (by default) to this pressure and is therefore considered to be 'Not sensitive'.

Salinity increase (local)	No evidence (NEv)	No evidence (NEv)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

No evidence.

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

Patella vulgata can tolerate varying salinities and its distribution extends into the mouths of estuaries surviving in salinities down to about 20 psu. However, growth and reproduction may be impaired in reduced salinity. Little *et al.* (1991), for example, observed reduced levels of activity in limpets after heavy rainfall and in the laboratory activity completely stopped at 12 psu. The species can endure periods of low salinity and was found to die only when the salinity was reduced to 3-1 psu (Fretter & Graham, 1994). In experiments where freshwater was trickled over the shell Arnold (1957) observed limpets withdrawing and clamping the shell onto the substratum. There appears to be an increasing tolerance of low salinities from the lower to the upper limit of distribution of the species on the shore (Fretter & Graham, 1994).

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).

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. The intertidal interstitial invertebrates

and epifauna probably experience short-term fluctuating salinities, with reduced salinities due to rainfall and freshwater runoff when emersed. Prolonged reduction in salinity, e.g. from full to reduced due to e.g. freshwater runoff, is likely to reduce the species richness of the biotope due to loss of less tolerant red algae and some intolerant invertebrates. However, the dominant species will probably survive and the integrity of the biotope is likely to be little affected. Areas of freshwater runoff in the intertidal promote the growth of ephemeral greens, probably due to their tolerance of low salinities and inhibition of grazing invertebrates.

Sensitivity assessment. Based on reported distributions and the results of experiments to assess salinity tolerance thresholds and behavioural and physiological responses in *Patella vulgata* and *Semibalanus balanoides* it is considered that the benchmark decrease in salinity (from full to variable) would not result in mortality of the characterizing species in biotopes that were previously fully marine. Resistance is therefore assessed as '**High**' and resilience as '**High**' (based on no effect to recover from) and the biotope is considered to be '**Not sensitive**' at the benchmark level.

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 exposed to moderately wave exposed conditions where water movement from wave action will greatly exceed the strength of any possible tidal flow. The evidence is presented for the tolerance of the key characterizing species, *Semibalanus balanoides* and *Patella vulgata* to changes in water flow. However, it should be noted that wave action, is more significant as an environmental factor than flow for this biotope.

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

Patella vulgata inhabits a range of tidal conditions and is, therefore, likely to tolerate a change in water flow rate. The streamlined profile of limpet shells is of importance in increasing their tolerance of water movement, and this is undoubtedly one factor in determining the different shape of limpets at different exposures. With increasing exposure to wave action, the shell

develops into a low profile reducing the risk of being swept away. The strong muscular foot and a thin film of mucus between the foot and the rock enables *Patella vulgata* to grip very strongly to the substratum (Fretter & Graham, 1994). The ability of limpets to resist accelerating, as distinct from constant currents, may set a limit to the kind of habitat in which they can occupy and limit the size to which they can grow.

Sensitivity assessment. The biotope is characteristic of exposed to moderately wave exposed conditions where water movement from wave action will greatly exceed the strength of any possible tidal flow. Based on the available evidence the characterizing species *Patella vulgata* and *Semibalanus balanoides* are able to adapt to high flow rates and the biotope is therefore considered to be '**Not sensitive**' to an increase in water flow. A decrease in water flow may have some effects on recruitment and growth, but this is not considered to be lethal at the pressure benchmark and resistance is therefore assessed as '**High**' and resilience as '**High**' (by default) so that the biotope is considered to be '**Not sensitive**'. A decrease in water flow, exceeding the pressure benchmark, coupled with a decrease in wave action, may, however, alter the character of the biotope to LR.MLR.MusF.MytFR or LR.MLR.MusF.MytFves, where brown seaweeds were able to proliferate and the edible periwinkle *Littorina littorea* was able to colonize.

Emergence regime changes

Low

Q: **Low** A: **NR** C: **NR**

Medium

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

Medium

Q: **Low** A: **Low** C: **Low**

Emergence regime is a key factor structuring this (and other) intertidal biotopes. Increased emergence may reduce habitat suitability for characterizing species through greater exposure to desiccation and reduced feeding opportunities for the barnacles which feed when immersed.

Semibalanus balanoides is less tolerant of desiccation stress than *Chthamalus* barnacles species and changes in emergence may, therefore, lead to species replacement and the development of a *Chthamalus* sp. dominated biotope, more typical of the upper shore may develop. Records suggest that, typically, above this biotope on the shore there may be a *Verrucaria maura* zone, or a band of *Chthamalus* sp. (Connor *et al.*, 2004). Changes in emergence may therefore eventually lead to the replacement of this biotope to one more typical of the upper shore.

Decreased emergence would reduce desiccation stress and allow the attached suspension feeders more feeding time. Predation pressure on mussels 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). Competition from large fucoids and red algal turfs can also prevent *Semibalanus balanoides* from extending into lower shore levels (Hawkins, 1983). Below this biotope, a community dominated by the wrack *Himanthalia elongata* and various red seaweeds such as *Corallina officinalis*, *Mastocarpus stellatus* and *Osmundea pinnatifida* often occurs (Connor *et al.*, 2004). Decreased emergence is likely to lead to the habitat the biotope is found in becoming more suitable for the lower shore species generally found below the biotope, leading to replacement.

The mobile species present within the biotope, including the characterizing species, *Patella vulgata* and *Nucella lapillus*, and the Littorinids would be able to relocate to preferred shore levels. Although the success of relocation by *Patella vulgata* may depend on shore rugosity and shell fit (see resilience section for further information).

Sensitivity assessment. Where this biotope occurs on the mid-shore it will be more sensitive to increased emergence, whereas lower shore examples may be more sensitive to decreased

emergence, as the changed conditions occur towards the margins of habitat tolerance. As emergence is a key factor structuring the distribution of animals on the shore, resistance to a change in emergence (increase or decrease) is assessed as '**Low**'. Resilience is assessed as '**Medium**', and sensitivity is therefore assessed as '**Medium**'.

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 moderately exposed or exposed (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 two 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 or decrease in wave action, exceeding the pressure benchmark, may, however, alter the character of the biotope. Where wave action was significantly reduced a biotope more typical of sheltered shores would be predicted to develop, e.g. LR.MLR.MusF.MytFR or LR.MLR.MusF.MytFves, where brown seaweeds were able to proliferate on the rock surfaces and the edible periwinkle *Littorina littorea* was able to colonize. A decrease in wave exposure may ultimately reduce *Patella vulgata* abundance because the species does not favour thick algal cover that is often present on very sheltered shores. Alternatively, an increase in significant wave height, linked to increased exposure, may result in population changes with fewer macroalgae present and with the limpet *Patella ulyssiponensis* present, or present in greater numbers, rather than *Patella vulgata* (Thompson, 1980) and *Chthamalus* sp. replacing *Semibalanus balanoides* (Ballantine, 1961).

Sensitivity assessment. The natural wave exposure range of this biotope is therefore considered to exceed changes at the pressure benchmark and this biotope is considered to have '**High**' resistance and '**High**' resilience (by default), and to be '**Not sensitive**' 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 a 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. In the Fal estuary *Patella vulgata* occurs at, or just outside, Restronguet Point at the end of the creek where metal concentrations are in the order: Zinc (Zn) 100-2000 µg/l, copper (Cu) 10-100 µg/l and cadmium (Cd) 0.25-5 µg/l (Bryan & Gibbs, 1983). However, in the laboratory, *Patella vulgata* was found to be

intolerant of small changes in environmental concentrations of Cd and Zn by Davies (1992). At concentrations of 10µg/l pedal mucus, production and levels of activity were both reduced, indicating a physiological response to metal concentrations. Exposure to Cu at a concentration of 100 µg/l for one week resulted in progressive brachycardia (slowing of the heart beat) and the death of limpets. Zn at a concentration of 5500 µg/l produced the same effect (Marchan *et al.*, 1999).

Hydrocarbon & PAH contamination

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

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

Hydrocarbon contamination, at levels greater than the benchmark, e.g. from spills of fresh crude oil or petroleum products, may cause significant loss of component species in the biotope, through impacts on individual species viability or mortality, and resultant effects on the structure of the community (Suchanek, 1993; Raffaelli & Hawkins, 1999). In areas of moderate oil deposit, up to about 1/2cm thick, on rocks after the *Torrey Canyon* oil spill, limpets had survived unscathed over a month after the event and feeding continued even though a coating of oil smothered their food source of algae and diatoms (Smith, 1968). Limpets can ingest thick oil and pass it through their gut. However, thick layers of oil smothering individuals will interfere with respiration and spoil normal food supplies for *Patella vulgata*. Limpets are unable to remain closed off from the environment for very long, the adductor muscles relax occasionally, lifting the shell very slightly. After the *Braer* oil spill, in common with many other oil spills, the major impact in the intertidal zone was on the population of limpets and other grazers. In West Angle Bay, where fresh oil from the *Sea Empress* tanker reached rocky shores within one day of the spill, limpet mortality was 90% (Glegg *et al.*, 1999). Thus *Patella vulgata* has a higher intolerance to fresh oil which has a high component of volatile hydrocarbons remaining. A significant reduction in the density of juvenile limpets was also observed at all sites known to have been oiled by the *Sea Empress* spill (Moore, 1997). In long-term studies into the environmental effects of oil refinery effluent discharged into Littlewick Bay, Milford Haven, the number of limpets, usually found in substantial numbers on this type of shore, were considerably reduced in abundance on areas close to the discharge (Petpiroon & Dicks, 1982). In particular, only large individuals were found close to the outfall point and juveniles were completely absent, suggesting that observed changes in abundance resulted from effluent effects on larval stages rather than upon adults directly.

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).

However, laboratory studies of the effects of oil and dispersants on several red algae species (Grandy, 1984 cited in Holt *et al.* 1995) concluded that they were all sensitive to oil/ dispersant mixtures, with little differences between adults, sporelings, diploid or haploid life stages. O'Brien & Dixon (1976) suggested that red algae were the most sensitive group of algae to oil or dispersant contamination.

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). Hoare & Hiscock (1974) reported that the limpet *Patella vulgata* was excluded from sites within 100-150m of the discharge of acidified, halogenated effluent in Amlwch Bay. Limpets are also extremely intolerant of aromatic solvent based dispersants used in oil spill clean-up. During the clean-up response to the *Torrey Canyon* oil spill nearly all the limpets were killed in areas close to dispersant spraying. Viscous oil will not be readily drawn in under the edge of the shell by ciliary currents in the mantle cavity, whereas detergent, alone or diluted in seawater, would creep in much more readily and be liable to kill the limpet (Smith, 1968). A concentration of 5ppm killed half the limpets tested in 24 hours (Southward & Southward, 1978; Hawkins & Southward, 1992). Acidified seawater affects the motility of *Patella vulgata*. At a pH of 5.5 motility was reduced whilst submerged but individuals recovered when returned to normal seawater. At a pH of 2.5 total inhibition of movement occurred and when returned to normal seawater half had died (Bonner *et al.*, 1993). Reduced motility reduces the time for foraging and may result in decreased survival of individuals. Acidified seawater can also change the shell composition which will lead to a decrease in its protective nature and hence survival (Bonner *et al.*, 1993). Short periods (48 hours) are unlikely to have much effect on a population but long periods (1 year) may cause reduced grazing and an increase in algal growth. However, seawater is unlikely to reach pH 2.5, therefore, intolerance to slight changes in pH will be low. Gastropod molluscs are known to be intolerant of endocrine disruption from synthetic chemicals such as tri-butyl tin (Cole *et al.*, 1999). However, no information on the specific effects of tri-butyl tin on *Patella vulgata* was found. Hoare & Hiscock (1974) reported that in Amlwch Bay *Patella vulgata* was excluded from sites within 100-150m of the discharge of acidified, halogenated effluent.

Red algae are probably intolerant of chemical contamination. O'Brien & Dixon (1976) suggested that red algae were the most sensitive group of algae to oil contamination, although the filamentous forms were the most sensitive. Laboratory studies of the effects of oil and dispersants on several red algae species, including *Palmaria palmata* (Grandy, 1984 cited in Holt *et al.*, 1995) concluded that they were all sensitive to oil/ dispersant mixtures, with little differences between adults, sporelings, diploid or haploid life stages. Cole *et al.* (1999) suggested that herbicides, such as simazine and atrazine were very toxic to macrophytes. In addition, Hoare & Hiscock (1974) noted that almost all red algae were excluded from Amlwch Bay, Anglesey by acidified halogenated effluent discharge.

Radionuclide contamination

No evidence (NEv)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

No evidence.

Introduction of other substances

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation

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

An oxygen concentration at the level of the benchmark, 2 mg/l, is thought likely to cause adverse effects in marine organisms. In laboratory experiments a reduction in the oxygen tension of seawater from 148 mm Hg (air saturated seawater) to 50 mm Hg rapidly resulted in reduced heart rate in limpets of the genus *Patella* (Marshall & McQuaid, 1993). Heartbeat rate returned to normal in oxygenated water within two hours. Limpets can survive for a short time in anoxic seawater; Grenon & Walker, (1981) found that in oxygen free water limpets could survive up to 36 hours, although Marshall & McQuaid (1989) found a lower tolerance for *Patella granularis*, which survived up to 11 hours in anoxic water. Therefore, some individuals may survive for one week at an oxygen concentration of 2 mg/l. However, *Patella vulgata* is an intertidal species, being able to respire in air, so would only be exposed to low oxygen in the water column intermittently during periods of tidal immersion. In addition, in areas of wave exposure and moderately strong current flow low oxygen levels in the water are unlikely to persist for very long.

Semibalanus balanoides can respire anaerobically, so they can tolerate some reduction in oxygen concentration (Newell, 1979). When placed in wet nitrogen, where oxygen stress is maximal and desiccation stress is low, *Semibalanus balanoides* have a mean survival time of 5 days (Barnes *et al.*, 1963).

Sensitivity assessment. The characterizing species *Patella vulgata* and *Semibalanus balanoides* are considered to be 'Not Sensitive' to deoxygenation at the pressure benchmark. Resistance is therefore assessed as 'High' and resilience as 'High' (no effect to recover from), resulting in a sensitivity of 'Not sensitive'. However, as this biotope occurs in the intertidal, emergence will mitigate the effects of hypoxic surface waters as will the exposure to wave action and water flows and this pressure is considered to be '**Not relevant**'.

Nutrient enrichment

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. 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. Limpets and other grazers would also benefit from increased growth of benthic microalgae. However, Holt *et al.* (1995) predict that smothering of barnacles by ephemeral green algae is a possibility under eutrophic conditions. However, if nutrient loading is excessive this can have a detrimental effect on algal productivity and hence limpet growth.

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, including the clumps of *Mytilus edulis*, are considered to be '**Not sensitive**' at the pressure benchmark. Resistance and resilience are therefore assessed as 'High'.

Organic enrichment

High

Q: High A: Low C: NR

High

Q: High A: High C: High

Not sensitive

Q: High 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 deoxygenation). The biotope 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. On the same shores, higher abundances of juvenile *Patella* sp. and lower abundances of adults were found closer to sewage inputs, Cabral-Oliveira *et al.*, (2014) suggested the structure of these populations was due to increased competition closer to the sewage outfalls.

Sensitivity assessment. Little empirical evidence was found to support an assessment for *Semibalanus balanoides* and *Patella vulgata* 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) with excess likely to be rapidly removed by wave action, 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'**. Limpets may be sensitive to even low levels of deposition (see siltation pressure), so that impacts from this pressure will depend on the duration of input and any deposits.

A Physical Pressures

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

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

Physical change (to another seabed type)	None Q: High A: High C: High	Very Low Q: High A: Medium C: High	High Q: High A: High C: Medium
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This biotope is characterized by the hard rock substratum to which the key characterizing species barnacles, *Semibalanus balanoides*, and limpets, *Patella vulgata*, and other species such as *Mytilus edulis* and algal turfs can firmly attach. A change to a sedimentary substratum would 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. The biotope is therefore considered to have **'None'** resistance to this pressure, resilience is **'Very low'** (the pressure is a permanent change) and sensitivity is assessed as **'High'**.

Physical change (to another sediment type)	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR
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Not relevant to biotopes occurring on bedrock.

Habitat structure changes - removal of substratum (extraction)

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

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

Abrasion/disturbance of the surface of the substratum or seabed

Low

Q: High A: Medium C: High

Medium

Q: High A: Medium C: High

Medium

Q: High A: Medium C: High

The barnacles and limpets that are the key characterizing species within this biotope typically occur on the rock surfaces where they will be exposed to abrasion. Although both species 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. Removal of limpets may result in these being displaced to a less favourable habitat and injuries to foot muscles may prevent reattachment. Evidence for the effects of abrasion is provided by a number of experimental studies on trampling (a source of abrasion) and on abrasion by wave thrown rocks and pebbles.

The effects of trampling on barnacles appear to be variable with some studies not detecting significant differences between trampled and controlled areas (Tyler-Walters & Arnold, 2008). However, this variability may be related to differences in trampling intensities and abundance of populations studied. The worst case incidence was reported by Brosnan and Crumrine (1994) who reported that a trampling pressure of 250 steps in a 20x20 cm plot one day a month for a period of a year significantly reduced barnacle cover at two study sites. Barnacle cover reduced from 66% to 7% cover in 4 months at one site and from 21% to 5% within 6 months at the second site. Overall barnacles were crushed and removed by trampling. Barnacle cover remained low until recruitment the following spring. Long *et al.* (2011) also found that heavy trampling (70 humans km⁻¹ shoreline h⁻¹) led to reductions in barnacle cover. Single step experiments provide a clearer, quantitative indication of sensitivity to direct abrasion. Povey & Keough (1991) in experiments on shores in Mornington Peninsula, Victoria, Australia, found that in single step experiments 10 out of 67 barnacles, (*Chthamalus antennatus* about 3 mm long), were crushed. However, on the same shore, the authors found that limpets may be relatively more resistant to abrasion from trampling. Following step and kicking experiments, few individuals of the limpet *Cellana trasomerica*, (similar size to *Patella vulgata*) suffered damage or relocated (Povey & Keough, 1991). One kicked limpet (out of 80) was broken and 2 (out of 80) limpets that were stepped on could not be relocated the following day (Povey & Keough, 1991). Trampling may lead to indirect effects on limpet populations, Bertocci *et al.*, (2011) found that the effects of trampling on *Patella* sp. increased the temporal and spatial variability of in abundance. The experimental plots were sited on a wave-sheltered shore dominated by *Ascophyllum nodosum*. On these types of shore, trampling in small patches, that removes macroalgae and turfs, will indirectly enhance habitat suitability for limpets by creating patches of exposed rock for grazing.

Shanks & Wright (1986), found that even small pebbles (<6 cm) that were thrown by wave action in Southern California shores could create patches in *Chthamalus fissus* aggregations and could smash owl limpets (*Lottia gigantea*). Average, estimated survivorship of limpets at a wave exposed site, with many loose cobbles and pebbles allowing greater levels of abrasion was 40% lower than at a

sheltered site. Severe storms were observed to lead to the almost total destruction of local populations of limpets through abrasion by large rocks and boulders.

Sensitivity assessment. The impact of surface abrasion will depend on the footprint, duration and magnitude of the pressure. Surface abrasion may directly crush and remove *Semibalanus balanoides* and *Patella vulgata*. Resistance is therefore assessed as '**Low**' for barnacles and limpets. Populations are predicted to recover within 2 - 10 years, so that resilience is considered to be '**Medium**' and sensitivity is '**Medium**'.

Penetration or disturbance of the substratum subsurface

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

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

Changes in suspended solids (water clarity)

Medium

Q: Low A: NR C: NR

High

Q: High A: Low C: High

Low

Q: Low A: Low C: Low

In general, increased suspended particles may enhance food supply (where these are organic in origin) or decrease feeding efficiency (where the particles are inorganic and require greater filtration efforts). Very high levels of silt may clog respiratory and feeding organs of the suspension feeding *Semibalanus balanoides* and clog the gills of *Patella vulgata*. In addition, increased turbidity will decrease light penetration reducing photosynthesis by macroalgae within this biotope. Increased levels of particles may increase scour and deposition in the biotope depending on local hydrodynamic conditions, although changes in substratum are assessed through the physical change (to another seabed type) pressure. Gyory *et al.* (2013) found that increased turbidity triggered the release of larvae by *Semibalanus balanoides*, a response that may allow the larval release to be timed with high levels of phytoplankton and at times where predation on larvae may be lowered due to the concentration of particles. Storm events that stir up sediments are also associated with the larval release (Gyory & Pineda, 2011).

A significant decrease in suspended organic particles may reduce food input resulting in reduced growth and fecundity of the suspension feeding barnacles. However, local primary productivity (phytoplankton and diatom films) may be enhanced where suspended sediments decrease, increasing food supply to both characterizing species. Decreased suspended sediment may increase macroalgal competition, enhancing diversity, but is considered unlikely to significantly change the character of the biotope as colonisation by larger brown macroalgae is likely to be limited by wave action in this biotope rather than light limitation.

Sensitivity assessment. The benchmark for this pressure refers to a change in turbidity of one rank on the Water Framework Directive (WFD) scale. Where changes in suspended sediment supply were linked to decreased wave action and water flow to enhance settlement, limpets would be sensitive to deposition (see siltation pressures). The biotope is considered to be 'Not sensitive' to a decrease in suspended solids. An increase in inorganic suspended sediments may negatively affect the feeding of *Semibalanus balanoides* with some impacts on growth and survival. Resistance is therefore assessed as '**Medium**' and resilience as '**High**' so that sensitivity is assessed as '**Low**'.

Smothering and siltation rate changes (light)**Low**

Q: High A: High C: High

Medium

Q: High A: Medium C: High

Medium

Q: High A: Medium C: High

More direct evidence to assess this pressure was found for the characterizing species *Patella vulgata*, 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).

Field observations and laboratory experiments have highlighted the sensitivity of limpets to sediment deposition (see also the 'heavy' siltation pressure for further information). Airolidi & Hawkins (2007) tested the effects of different grain sizes and deposit thickness in laboratory experiments using *Patella vulgata*. Sediments were added as a 'fine' rain to achieve deposit thicknesses of approximately 1mm, 2 mm, and 4 mm in controlled experiments and grazing and mortality observed over 8-12 days. Limpets were more sensitive to sediments with a higher fraction of fines (67% silt) than coarse (58% sand). Coarse sediments of thicknesses approximately 1, 2 and 4 mm decreased grazing activity by 35, 45 and 50 % respectively. At 1 and 2 mm thicknesses, fine sediments decreased grazing by 40 and 77 %. The addition of approximately 4 mm of fine sediment completely inhibited grazing. Limpets tried to escape the sediment but lost attachment and died after a few days (Airolidi & Hawkins, 2007).

Observations on exposed and sheltered shores with patches of sediment around Plymouth in the south-west of England found that *Patella vulgata* abundances were higher where deposits were absent. The limpets were locally absent in plots with 50-65% sediment cover (Airolidi & Hawkins, 2007). Littler *et al.* (1983) found that another limpet species, *Lottia gigantea* on southern Californian shores was restricted to refuges from sand burial on shores subject to periodic inundation by sands.

Sensitivity assessment. *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 is assessed as 'Medium' as wave action on rocky shores is likely to rapidly mobilise and remove deposits alleviating the effect of smothering. Resilience is assessed as 'High' and sensitivity is therefore considered to be 'Low'.

Even small deposits of sediments are likely to result in local removal of limpets. The level of impact will depend on the magnitude and duration of impact. It should be noted that the level of exposure may be reduced by wave action or water flows so that site-specific vulnerability will be lower where sediments do not accumulate. Resistance to siltation is assessed as 'Low' for *Patella vulgata* based primarily on observations and experiments of Airolidi & Hawkins, (2007), who demonstrated negative effects at deposit thicknesses far lower than the pressure benchmark. Small patches subject to a single impact may recover rapidly via adult migration. However, based on the prolonged recovery times experienced in more wide-ranging impacts, resilience is assessed as 'Medium' (2-10 years) and sensitivity is therefore assessed as 'Medium'. This more precautionary assessment is presented for the biotope, rather than the lower sensitivity of *Semibalanus balanoides*. Repeated deposition events, coupled with changes in water flow and wave action may lead to the establishment of turf-forming algae that trap sediments, this would significantly alter the character of the biotope.

Smothering and siltation rate changes (heavy)**None**

Q: High A: High C: High

Medium

Q: High A: Medium C: High

Medium

Q: High A: Medium C: High

More direct evidence to assess this pressure was found for the characterizing species *Patella vulgata*, 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). Barnacle feeding may be affected however by smothering, wave action on rocky shores is likely to rapidly mobilise and remove deposits alleviating the effect of smothering. 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).

Field observations and laboratory experiments have highlighted the sensitivity of limpets to sediment deposition (see also the 'heavy' siltation pressure for further information). Airoidi & Hawkins (2007) tested the effects of different grain sizes and deposit thickness in laboratory experiments using *Patella vulgata*. Sediments were added as a 'fine' rain to achieve deposit thicknesses of approximately 1mm, 2 mm, and 4 mm in controlled experiments and grazing and mortality observed over 8-12 days. Limpets were more sensitive to sediments with a higher fraction of fines (67% silt) than coarse (58% sand). Coarse sediments of thicknesses approximately 1, 2 and 4 mm decreased grazing activity by 35, 45 and 50 % respectively. At 1 and 2 mm thicknesses, fine sediments decreased grazing by 40 and 77 %. The addition of approximately 4 mm of fine sediment completely inhibited grazing. Limpets tried to escape the sediment but lost attachment and died after a few days (Airoidi & Hawkins, 2007). Observations on exposed and sheltered shores with patches of sediment around Plymouth in the south-west of England found that *Patella vulgata* abundances were higher where deposits were absent. The limpets were locally absent in plots with 50-65% sediment cover (Airoidi & Hawkins, 2007). Littler *et al.*, (1983) found that another limpet species, *Lottia gigantea* on southern Californian shores was restricted to refuges from sand burial on shores subject to periodic inundation by sands.

Sensitivity assessment. 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. Resilience is assessed as 'Medium' and sensitivity is therefore considered to be 'Medium'. No direct evidence for sensitivity to siltation was found. However, mortality will depend on the duration of smothering, where wave action rapidly mobilises and removes fine sediments, survival may be much greater. Even small deposits of sediments are likely to result in local removal of limpets. Resistance to siltation at the benchmark level is assessed as '**None**' for *Patella vulgata* based primarily on the observations and experiments of Airoidi & Hawkins, (2007), who demonstrated negative effects at deposit thicknesses far lower than the pressure benchmark. Small patches subject to a single impact may recover rapidly via adult migration. However, based on the prolonged recovery times experienced in more wide-ranging impacts, resilience is assessed as '**Medium**' (2-10 years) and sensitivity is therefore assessed as '**Medium**'. This more precautionary assessment is presented for the biotope, rather than the lower sensitivity of *Semibalanus balanoides*. Repeated deposition events, coupled with changes in water flow and wave action may lead to the establishment of turf-forming algae that trap sediments, this would significantly alter the character of the biotope.

Litter

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

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

Electromagnetic changes

No evidence (NEv)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

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

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

Barrier to species movement

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 *Patella vulgata* and *Semibalanus balanoides* 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. As both 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 assessed as '**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

Not relevant (NR)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

The characterizing species, *Semibalanus balanoides* and *Patella vulgata* 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 1-2 cm in length) from wild populations, with subsequent transportation around the UK for re-laying in suitable habitats. As the seed is harvested from wild populations from various locations the gene pool will not necessarily be decreased by translocations. Movement of mussel seed has the potential to transport pathogens and non-native species (see 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 wild individuals 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 gene flow between cultivated beds and local wild populations, there is currently no evidence to assess the impact (Svåsand *et al.*, 2007).

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

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

Sensitivity assessment. Overall, there is little evidence of this biotope being adversely affected by non-native species, resistance is therefore assessed as '**High**', and resilience as '**High**' (by default), and the biotope is considered to be '**Not sensitive**'.

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 *Semibalanus balanoides* and *Patella vulgata* are considered 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. *Patella vulgata* has been reported to be infected by the protozoan *Urceolaria patellae* (Brouardel, 1948) at sites sheltered from extreme wave action in Orkney. Baxter (1984) found shells to be infested with two boring organisms, the polychaete *Polydora ciliata* and a siliceous sponge *Cliona celata*.

Sensitivity assessment. Based on the characterizing species, *Semibalanus balanoides* and *Patella vulgata*, 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: Low A: NR C: NR

Low

Q: High A: Medium C: High

High

Q: Low A: Low C: Low

The species *Mytilus edulis* is too small and patchy in this biotope to be targeted for commercial harvesting. However, some unregulated recreational hand-gathering of this species and the limpet *Patella vulgata* may occur. Gathering of *Mytilus edulis* is not considered to affect the biotope as this species is present in low densities, as small individuals in cracks and crevices and is therefore not a key characterizing or structuring species. *Patella vulgata*, however, is a key characterizing and structuring species within this biotope. *Patella vulgata* grazing can control the character of the shore by grazing algae and newly settled barnacle larvae. Even a small, localised temporary absence of limpets (Southward, 1956; Southward, 1964; Hawkins, 1981; Hawkins *et al.*, 1983) can alter the biological assemblage. Significant limpet kills resulting from the widespread use of dispersants after the *Torrey Canyon* oil spill dramatically altered rocky shore communities. *Laminaria digitata*, for example, was able to extend 2 m up the shore in the absence of limpets and there were dense growths of ephemeral green seaweeds followed by equally dense growth of fucoids (Southward & Southward, 1978; Hawkins & Southward, 1992).

Sensitivity assessment. LR.HLR.MusB.Sem.Sem is characterized by the limpet *Patella vulgata*.

Patella vulgata is considered a key structuring species within the barnacle and limpet dominated biotope, LR.HLR.MusB.Sem.Sem, as its grazing (coupled with wave action), maintains the bare rock surfaces allowing colonization by *Semibalanus balanoides* and prevents a denser algal turf developing. The resistance of *Patella vulgata* to removal is 'Low' as this species is relatively large and is immobile and therefore easily found and removed. Recovery (of the species and biotope) is assessed as 'Low' (10-20 years) as an alternate stable state may develop (see resilience section) so that sensitivity is assessed as 'High'. It should be noted that the assessment refers to a single event, sensitivity to persistent, on-going collection could be higher. The removal of *Patella vulgata* may allow the variant LR.HLR.MusB.Sem.FvesR to develop.

Removal of non-target species

Low

Q: Low A: NR C: NR

Medium

Q: High A: Medium C: High

Medium

Q: Low A: Low C: Low

The characterizing species *Mytilus edulis* is too small and patchy in this biotope to be targeted for commercial harvesting. However, some hand-gathering of this species and the edible periwinkle *Littorina littorea* may occur. As *Littorina littorea* are present only in low densities and the biotope is wave exposed, ecological effects such as the proliferation of algae are not predicted to arise from its removal. Removal of the characterizing species, limpets and barnacles and the red seaweeds accidentally would alter the character of the biotope. The ecological services such as filtration and primary and secondary production provided by these species would also be lost.

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 resilience as 'Medium', so that sensitivity is assessed as 'Medium'.

Bibliography

- 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.
- 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., 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., Finlayson, D.M. & Piatigorsky, J., 1963. The effect of desiccation and anaerobic conditions on the behaviour, survival and general metabolism of three common cirripedes. *Journal of Animal Ecology*, **32**, 233-252.
- Barnes, M., 2000. The use of intertidal barnacle shells. *Oceanography and Marine Biology: an Annual Review*, **38**, 157-187.
- Baxter, J.M., 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., Wiczorek, 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. Marteilioidosis 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.
- 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 success. 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.
- 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.
- Burrows, E.M., 1991. *Seaweeds of the British Isles. Volume 2. Chlorophyta*. London: British Museum (Natural History).
- 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.
- 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.
- Crothers, J.H., 1985. Dog-whelks: an introduction to the biology of *Nucella lapillus* (L.) *Field Studies*, **6**, 291-360.
- 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, G., Dare, P.J. & Edwards, D.B., 1980. Fenced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore crabs (*Carcinus maenas* (L.)) in Morecambe Bay, England. *Ministry of Agriculture, Fisheries and Food. Fisheries Technical Report*, no. 56.
- Davies, M.S., 1992. Heavy metals in seawater: effects on limpet pedal mucus production. *Water Research*, **26**, 1691-1693.
- Davies, S.P., 1970. Physiological ecology of *Patella* IV. Environmental and limpet body temperatures. *Journal of the Marine*

- Biological Association of the United Kingdom, **50** (04), 1069-1077.
- de Vooy, C.G.N., 1987. Elimination of sand in the blue mussel *Mytilus edulis*. *Netherlands Journal of Sea Research*, **21**, 75-78.
- 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.
- 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.
- 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 furoid/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.
- 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.
- 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., Åberg, 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 furoid 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, 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 Ecology*, **364** (1), 1-10.
- Landsberg, J.H., 1996. Neoplasia and biotoxins in bivalves: is there a connection? *Journal of Shellfish Research*, **15**, 203-230.
- 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.
- 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.
- 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.
- 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 granularis* (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 R.*, **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.
- 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.
- 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. & 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.
- 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.
- 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.
- 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)*.
- 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
- 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.
- 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.
- 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.