

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

Saccharina latissima with *Psammechinus miliaris* and/or *Modiolus modiolus* on variable salinity infralittoral sediment

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

Thomas Stamp

2015-10-12

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

Please note. This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [https://www.marlin.ac.uk/habitats/detail/1036]. All terms and the MarESA methodology are outlined on the website (https://www.marlin.ac.uk)

This review can be cited as:

Stamp, T.E., 2015. [Saccharina latissima] with [Psammechinus miliaris] and/or [Modiolus modiolus] on variable salinity infralittoral sediment. 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.1036.1



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



(page left blank)

Saccharina latissima with Psammechinus miliaris and/or Modiolus modiolus on variable salinity infralittoral sediment - Marine Life Information Network



Researched by Thomas Stamp Refereed by Admin

Summary

UK and Ireland classification

EUNIS 2008	A5.523	Laminaria saccharina with Psammechinus miliaris and/or Modiolus modiolus on variable salinity infralittoral sediment
JNCC 2015	SS.SMp.KSwSS.SlatMxVS	Saccharina latissima with Psammechinus miliaris and/or Modiolus modiolus on variable salinity infralittoral sediment
JNCC 2004	SS.SMp.KSwSS.LsacMxVS	Laminaria saccharina with Psammechinus miliaris and/or Modiolus modiolus on variable salinity infralittoral sediment
1997 Biotope	1	



Shallow kelp community found on stoney mixed sediment, in full or variable salinity, in sheltered or moderately exposed conditions, with weak or very weak tidal currents. The community is characterized by a dense covering of *Saccharina latissima*. Beneath the kelp canopy, frequent *Psammechinus miliaris* may be found grazing the algal turf and scattered *Modiolus modiolus* are characteristic of this biotope. Encrusting the suface of stones and pebbles are *Spirobranchus triqueter* and in the sediment between the stones, the burrowing anemone *Cerianthus lloydii* may also be present. Small patches of *Lithothamnion glaciale* may be found in this biotope, although these patches do not form distict beds as in SBR.Lgla. In addition, a more ubiquitous fauna such as *Asterias rubens* and *Pagurus bernhardus* are also present. This biotope is generally found in sealochs.

↓ Depth range

-

Additional information

-

✓ Listed By

- none -

% Further information sources

Search on:

G S G JNCC

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

SS.SMp.KSwSS.SlatMxVS typically occurs on a mixture of shallow sediments and rock fractions in both full and variable salinity, in sheltered or moderately exposed conditions, in predominantly weak-very weak tidal streams (<0.5m/s). The biotope is characterized by a dense *Saccharina latissima* canopy, frequent *Psammechinus miliaris* grazing on an algal turf and sparse *Modiolus modiolus*. Loss of any or all of these characteristic species would result in a major change in the character of, or loss of, the biotope.

In undertaking this assessment of sensitivity, account is taken of knowledge of the biology of all characterizing species in the biotope. For this sensitivity assessment *Saccharina latissima*, *Psammechinus miliaris* and *Modiolus modiolus* are the primary foci of research, however it is recognized that the understory algal turf are also an important feature of the biotope. Examples of important species groups are mentioned where appropriate.

Resilience and recovery rates of habitat

Saccharina lattisima is a perennial kelp characteristic of wave sheltered sites of the North East Atlantic, distributed from northern Portugal to Spitzbergen, Svalbard (Birkett et al., 1998; Conor et al., 2004; Bekby & Moy, 2011; Moy & Christie, 2012). Saccharina lattisima is capable of reaching maturity within 15-20 months (Sjøtun, 1993) and has a life expectancy of 2-4 years (Parke, 1948). Maximum growth has been recorded in late winter early spring, in late summer and autumn growth rates slow (Parke, 1948; Lüning, 1979; Birkett et al., 1998). The overall length of the sporophyte may not change during the growth season due to marginal (distal) erosion of the blade, but extension growth of the blade has been measured at 1.1 cm/day, with total length addition of over 2.25 m of tissue per year (Birkett et al., 1998). Saccharina latissima has a heteromorphic life strategy. Vast numbers of zoospores are released from sori located centrally on the blade between autumn and winter. Zoospores settle onto rock substrata and develop into dioecious gametophytes (Kain, 1979) which, following fertilization, germinate into juvenile sporophytes from winter-spring. Kelp zoospores are expected to have a large dispersal range, however, zoospore density and the rate of successful fertilization decreases exponentially with distance from the parental source (Fredriksen et al., 1995). Hence, recruitment following disturbance can be influenced by the proximity of mature kelp beds producing viable zoospores to the disturbed area (Kain, 1979; Fredriksen et al., 1995).

In 2002 a 50.7-83% decline of *Saccharina latissima* was discovered in the Skaggerak region, South Norway (Moy *et al.*, 2006; Moy & Christie, 2012). Survey results indicated a sustained shift from *Saccharina latissima* communities to those of ephemeral filamentous algal communities. The reason for the community shift was unknown, low water movement in wave and tidally sheltered areas combined with the impacts of dense human populations, e.g. increased land run-off, was suggested to be responsible for the dominance of ephemeral turf macro-algae. Multiple stressors such as eutrophication, increasing regional temperature, increased siltation and overfishing may also be acting synergistically to cause the observed habitat shift.

A large pressure for *Laminaria hyperborea* biotopes (e.g. IR.HIR.KFaR.LhypR) is urchin grazing pressure, particularly from the species *Echinus esculentus*, *Paracentrotus lividus* and *Strongylocentrotus droebachiensis*. Multiple authors (Steneck *et al.*, 2002; Steneck *et al.*, 2004; Rinde & Sjøtun, 2005; Norderhaug & Christie, 2009; Smale *et al.*, 2013) have reported dense

aggregations of sea urchins to be a principal threat to *Laminaria hyperborea* biotopes of the North Atlantic. Intense urchin grazing creates expansive areas known as "urchin barrens", in which a shift can occur from *Laminaria hyperborea* dominated biotopes to those characterized by coralline encrusting algae, with a resultant reduction in biodiversity (Lienaas & Christie, 1996; Steneck *et al.*, 2002, Norderhaug & Christie, 2009). Continued intensive urchin grazing pressure on *Laminaria hyperborea* biotopes can inhibit the *Laminaria hyperborea* recruitment (Sjøtun *et al.*, 2006) and cause urchin barrens to persist for decades (Cristie *et al.*, 1998; Stenneck *et al.*, 2004; Rinde & Sjøtun, 2005). A kelp recolinization experiment conducted by Lienaas & Christie (1996) removed *Strongylocentrotus droebachiensis* from "urchin barrens" and observed a succession effect. Within the experiment it was observed that the substratum was initially colonized by filamentous macroalgae and within 2 weeks *Saccharina latissima* colonized and persisted for 2 years. However after 2-4 years *Laminaria hyperborea* dominated the community. Despite *Laminaria hyperborea's* eventual dominance within the community Lienaas & Christie (1996) demonstrated that *Saccharina latissima* can colinse cleared areas rapidly.

Psammechinus miliaris is a sea urchin distributed across the north east Atlantic from Morocco to northern Scandinavia (Mortensen, 1927). In the British Isles it can occur in dense aggregation within sheltered locations e.g. Scottish sea lochs, and its distribution frequently coincides with that of *Saccharina latissima* (Kelly, 2000). *Psammechinus miliaris* grazes on a wide array of algae and encrusting organisms, including live *Saccharina latissima* (as in IR.LIR.KVS.SlatPsaVS) (Kelly, 2000; Connor *et al.*, 2004). *Psammechinus miliaris* can reach sexual maturity within the first year, reproduce each successive year (Elmhirst, 1922) and are reported to live up 10 years (Allain, 1978). Gametogenesis begins in May and spawning usually occurs between June and August. Depending on food availability, planktonic larvae will then typically settle out within 20-21 days, 5-7 days after settlement the gut will fully developed and juveniles will begin grazing (Kelly, 2001).

Modiolus modiolus is a large bivalve with a wide UK distribution (NBN gateway, 2015). Modiolus modiolus is adapted to live semi-infaunally with an endobyssate attachment to the substratum but may also be found attached to hard substratum, epifaunally in a manner similar to the common mussel Mytilus edulis. Modiolus modiolus can form expansive beds which vary in size, density, thickness and form. However within SS.SMp.KSwSS.SlatMxVS only sparse individuals are present. Individuals over 25 years old are frequent in British populations, with occasional records of individuals of up to 35 years old. The maximum life expectancy is thought to be in excess of 50 years (Anwar et al., 1990). The spawning season is variable or unclear and varies with depth and geographic location, probably related to temperature (de Schwienitz & Lutz, 1976; reviewed by Brown, 1984; Holt et al., 1998). For example: in Strangford Lough, Ireland the population exhibits a slow, continuous release of gametes (Seed & Brown, 1977; Brown & Seed, 1977); populations off south east of the Isle of Man show an annual gametogenesis and spawning cycle, with continuous release of gametes and a peak in spring and summer (Jasim & Brand; 1989); Scottish populations showed a slow release of gametes throughout the year with peaks of spawning in spring and summer in some areas (Comely, 1978); Swedish and northern Norwegian populations showed a distinct spawning in June-July respectively (Brown, 1984), and Wiborg (1946) reported that spawning occurring only every 2nd to 3rd year in Norwegian waters. Brown (1984) suggested that Modiolus modiolus commenced spawning over a narrow range of temperatures (7 - 10°C), timed with suitable conditions for larval development. Brown (1984) also suggested that the suitable spawning temperature may limit this species' northern distribution.

Recruitment in Modiolus modiolus is sporadic and highly variable seasonally, annually or with location (geographic and depth) (Holt et al 1998). Some areas may have received little or no recruitment for several years. Even in areas of regular recruitment, such as enclosed areas,

recruitment is low in comparison with other mytilids such as Mytilus edulis. For instance, in Strangford Lough, small horse mussels (<10mm) represented <10% of the population, with peaks of 20-30% in good years (Brown & Seed 1977). In open areas with free water movement larvae are probably swept away from the adult population, and such populations are probably not selfrecruiting but dependant on recruitment from other areas, which is in turn dependant on the local hydrographic regime. In addition, surviving recruits take several to many years to reach maturity (3-8 years) (Holt et al 1998). However, colonization on new structures such as the legs of oil rigs can occur within a few years (K. Hiscock pers. comm., cited from Holt et al 1998).

Modiolus modiolus recruitment is sporadic and highly variable seasonally, annually or with location (geographic and depth) (Holt et al 1998). Some areas may have received little or no recruitment for several years. Even in areas of regular recruitment, such as enclosed areas, recruitment is low in comparison with other mytilids such as Mytilus edulis. In open coast areas, e.g. the Llyn Peninsula and Sarnau, released larvae are probably swept away from the adult population (Comely, 1978; Holt et al., 1998). Holt et al. (1998) cite unpublished preliminary genetic data that suggest that beds off the south east of the Isle of Man receive recruits from other areas, albeit in a sporadic manner. Holt et al. (1998) suggested that enclosed areas such as Strangford Lough and the Scottish sea lochs would be relatively self sustaining. For instance, in Strangford Lough, small horse mussels (<10mm) represented <10% of the population, with peaks of 20-30% in good years (Brown & Seed 1977). In open areas with free water movement larvae are probably swept away from the adult population, and such populations are probably not self-recruiting but dependant on recruitment from other areas, which is in turn dependant on the local hydrographic regime. In addition, surviving recruits take several to many years to reach maturity (3-8 years) (Holt et al 1998). However, colonization on new structures such as the legs of oil rigs can occur within a few years (K. Hiscock pers. comm., cited from Holt et al 1998; Tillin & Tyler-Walters, 2014).

Translocation of horse mussels *Modiolus modiolus*, to areas of 'cultch' (broken scallop shells) in Strangford Lough, Northern Ireland as part of a programme of work to restore populations destroyed by scallop dredging, indicated that settlement of *Modiolus modiolus* larvae was directly enhanced by the presence of adults on the sea floor (Davoult *et al.*, 1990). Translocation seemed essential and, as a part of the same study, Elsäßer *et al.* (2013) concluded that remnant populations of *Modiolus modiolus* are largely self-recruiting with little connectivity between them and with populations outside the lough. They suggested that the best approach to accelerate the recovery and restoration of *Modiolus modiolus* biogenic reefs in Strangford Lough is to provide total protection of all remaining larval sources and establish additional patches of mussels in areas where models predicted certain larval densities to ensure that restoration sites are located where recovery has the highest likelihood of success (Tillin & Tyler-Walters, 2014).

Growth rates have been inferred from growth rings. Growth is rapid in the first 4-6 years, with energy being diverted to growth rather than reproduction. Rapid juvenile growth appears to be an adaptation to avoid predation. Once large size has been reached growth is very slow. Once individuals reach 45-60 mm in length they become relatively immune to predation as only the very largest crabs and starfish can open horse mussels over 50mm in length (Seed & Brown, 1978; Anwar et al., 1990; Holt et al., 1998). Sexual maturity occurs at about 35-40 mm according to Anwar et al. (1990) and coincides approximately with the size, at which individuals become less prone to predation and can divert resources to growth (Brown & Seed, 1977). Reported ages at maturation vary and include: 3-4 years of age in the Isle of Man (Jasim, 1986); 5-6 years in Norwegian waters (Wiborg, 1946); 7-8 years in Canadian populations (Rowell, 1967), and over 4 years of age in Strangford Lough (Seed & Brown, 1978).

Resilience assessment. *Psammechinus miliaris* can become sexually mature with its first year, although recruitment in echinoderms is sporadic or variable depending on locality. *Saccharina latissima* also has rapid recovery rates, recovering from *Strongylocentrotus droebachiensis* 'urchin Barrens' appearing after a few weeks, and can reach maturity within 15-20 months (Birkett et al., 1998). UK populations of *Modiolus modiolus*, populations demonstrate sporadic and highly variable recruitment, slow growth and can take 3-8 years to reach maturity. The resilience of *Modiolus modiolus modiolus* reefs is regarded as 'Very low' or 'Low' (10-25 years) (Tillin & Tyler-Walters, 2014). However, the abundance of *Modiolus modiolus* is only recorded as occasional in SS.SMp.KSwSS.SlatMxVS; an abundance that may require only limited recruitment to maintain or recover. Therefore, the resilience of the biotope has been assessed as '**Medium**'. Please note some pressures may affect some of the characterizing species over others resilience scores may therefore vary throughout this review.

🏦 Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	Low Q: High A: High C: High	Medium Q: High A: High C: High	<mark>Medium</mark> Q: High A: High C: High
(local)	Q: High A: High C: High	Q: High A: High C: High	Q: High A: High C: High

The temperature isotherm of 19-20°C has been reported as limiting *Saccharina latissima* geographic distribution (Müller *et al.*, 2009). Gametophytes can develop in \leq 23°C (Lüning, 1990) however, the optimal temperature range for sporophyte growth is 10-15°C (Bolton & Lüning, 1982). Bolton & Lüning (1982) observed that sporophyte growth was inhibited by 50-70% at 20°C and following 7 days at 23°C all specimens completely disintegrated. In the field *Saccharina latissima* has shown significant regional variation in its acclimation to temperature changes, for example Gerard & Dubois (1988) observed sporophytes of *Saccharina latissima* which were regularly exposed to \geq 20°C could tolerate these temperatures, whereas sporophytes from other populations which rarely experience \geq 17°C showed 100% mortality after 3 weeks of exposure to 20°C. Therefore the response of *Saccharina latissima* to a change in temperatures is likely to be locally variable.

Andersen *et al.* (2011) transplanted *Saccharina latissima* in the Skagerrak region, Norway and from 2006-2009. There was annual variation however high mortality occurred from August-November within each year of the experiment. In 2008 of the original 17 sporophytes 6 survived from March-September (approx. 65% mortality rate). All surviving sporophytes were heavily fouled by epiphytic organisms (estimated cover of 80 & 100%). Between 1960 and 2009, sea surface temperatures in the region have regularly exceeded 20°C and so has the duration which temperatures remain above 20°C. High sea temperature has been linked to slow growth of *Saccharina latissima* which is likely to decrease the photosynthetic ability of, and increase the vulnerability of *Saccharina latissima* to epiphytic loading, bacterial and viral attacks (Anderson *et al.*, 2011). These factors combined with establishment of annual filamentous algae in Skagerrak, Norway are likely to prevent the establishment of self sustaining populations in the area (Anderson *et al.*, 2011; Moy & Christie, 2012).

Mortensen (1927) reported *Psammechinus miliaris* was found in Limfjorden, Denmark where winter temperatures are regularly just above 0°C (Ursin, 1960). At *Psammechinus miliaris* southern range edge, Morocco and the Azores (Mortensen, 1927), winter-summer seawater temperatures range from17-21 °C (Sea temperature, 2015). Furthermore *Psammechinus miliaris* reproduces in waters around the Faeroes where the summer temperatures seldom exceed 11°C (Ursin, 1960). The

optimal temperature tolerance is therefore likely to be between 0-21°C.

Modiolus modiolus is a boreal species that reaches its southern limit in UK waters and forms beds of large individuals only in the north of Britain and Ireland (Hiscock *et al.*, 2004). The depth range of *Modiolus modiolus* increases at higher latitudes with intertidal specimens more common on northern Norwegian shores where air temperatures are lower (Davenport & Kjørsvik, 1982). Little direct information on temperature tolerance in *Modiolus modiolus* was found, however, its upper lethal temperature is lower than that for *Mytilus edulis* (Bayne, 1976) by about 4°C (Henderson, 1929, cited in Davenport & Kjørsvik, 1982). Subtidal populations are protected from major, short-term changes in temperature by their depth. However, Holt *et al.* (1998) suggested that because *Modiolus modiolus* modiolus reaches its southern limit in British waters it may be susceptible to long-term increases in summer water temperatures. Hiscock *et al.* (2004) suggest that warmer seas may prevent recovery of damaged beds and recruitment to undamaged beds so that decline in occurrence of beds can be expected at least in the south of their range. Declines of horse mussel beds in Strangford Lough (Magorrian, 1995) may be linked to increased water temperatures but other factors such as trawling have also contributed to changes.

SS.SMp.KSwSS.SlatMxVS is distributed from the west coast of Scotland to Shetland (Connor *et al.*, 2004). At this latitude sea surface temperature ranges from 14.5-16.9°C in summer and 4-10°C in winter (Beszczynska-Möller & Dye, 2013).

Sensitivity assessment. A 5°C increase for one month combined with high UK summer temperatures may cause mortality in *Saccharina latissima* populations that are not acclimated to >20°C. *Modiolus modiolus* is a boreal species, and the fact that dense aggregations seem to reach their southerly limit around British shores suggests this species would be sensitive to acute and chronic increases in temperature. Resistance has been assessed as **Low** and resilience as **Medium**. Sensitivity has been assessed as **Medium**.

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

Saccharina lattissima has a lower temperature threshold for sporophyte growth at 0°C (Lüning, 1990). Mortensen (1927) reported *Psammechinus miliaris* was found in Limfjorden, Denmark where winter temperatures are regularly just above 0°C. *Modiolus modiolus* is a boreal species that reaches its southern limit in UK waters and forms beds of large individuals only in the north of Britain and Ireland (Hiscock *et al.*, 2004). Davenport & Kjørsvik (1982) suggested that its inability to tolerate temperature change was a factor preventing *Modiolus modiolus* from colonizing the intertidal in the UK. Intertidal specimens were more common on northern Norwegian shores (Davenport & Kjørsvik, 1982). Subtidal populations are protected from major, short-term changes in temperature by their depth. Subtidal red algae can survive at temperatures between -2°C and 18-23°C (Lüning, 1990; Kain & Norton, 1990).

Sensitivity assessment. None of the characterizing species are likely to be adversely affected by a temperature decrease at the benchmark level. Resistance has been assessed as '**High**', resilience as '**High**' and sensitivity as '**Not sensitive**'.

Saccharina latissima with Psammechinus miliaris and/or Modiolus modiolus on variable salinity infralittoral sediment -Marine Life Information Network

Salinity increase (local)



High Q: High A: Medium C: High Medium

Q: Medium A: Medium C: High

Karsten (2007) tested the photosynthetic ability of *Saccharina latissima* under acute 2 and 5 day exposure to salinity treatments ranging from 5-60 psu. A control experiment was also carried at 34 psu. *Saccharina latissima* showed high photosynthetic ability at >80% of the control levels between 25-55 psu. The affect of long-term salinity changes (>5 days) or salinity >60 PSU on *Saccharina latissima*' photosynthetic ability was not tested.

Gezelius (1963) reported mature individuals of the littoral growth form of *Psammechinus miliaris* had an optimal salinity range of 20-32ppt but could tolerate 40ppt, and the sub-littoral growth form had an optimal salinity tolerance of 26-38 ppt but could tolerate as high as 40 ppt.

Modiolus modiolus are osmoconfers, in short-term fluctuating salinities valve closure limits exposure to salinity changes in the surrounding waters, although slow diffusion through the byssal aperture means that the osmolarity of fluids will eventually increase (Shumway, 1977; Davenport & Kjørsvik,1982). Experimental evidence for short-term tolerances of *Modiolus modious* to increased salinities is provided by Pierce (1970). *Modiolus modious* was exposed to a range of salinities between 1.5 and 54 psu and survived for 21 days (the duration of the experiment) at salinities between 27 and 41‰ However above 41‰ was considered lethal, and 50% of the individuals within the hypersaline? experiments died(Pierce, 1970).

Sensitivity assessment. SS.SMp.KSwSS.SlatMxVS is found in both full and variable salinity, this assessment assumes an increase to greater than full salinity (>40‰). The evidence suggests *Saccharina latissima* can tolerate exposure to hypersaline conditions of 55‰ for short periods however the effects of long-term salinity increases are unknown. >40‰ would be outside *Psammechinus miliaris* optimal salinity range and may cause minor declines in growth. *Modiolus modiolus* abundance may also decline. Resistance has been assessed as 'Low', resilience as 'Medium'. The sensitivity of this biotope to an increase in salinity has been assessed as 'Medium'.

Salinity decrease (local)

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

Q: Medium A: Medium C: Medium

Karsten (2007) tested the photosynthetic ability of *Saccharina latissima* under acute 2 and 5 day exposure to salinity treatments ranging from 5-60 psu. A control experiment was also carried at 34 psu. *Saccharina latissima* showed high photosynthetic ability at >80% of the control levels between 25-55 psu. Hyposaline treatment of 10-20 psu led to a gradual decline of photosynthetic ability. After 2 days at 5 psu *Saccharina latissima* showed a significant decline in photosynthetic ability at approx. 30% of control. After 5 days at 5 psu *Saccharina latissima* specimens became bleached and showed signs of severe damage. The affect of long-term salinity changes (>5 days) or salinity >60 PSU on *Saccharina latissima*' photosynthetic ability was not tested. The experiment was conducted on *Saccharina latissima* from the Arctic, and at extremely low water temperatures (1-5°C) macroalgae acclimation to rapid salinity changes could be slower than at temperate latitudes. It is therefore possible that resident *Saccharina latissima* of the UK maybe be able to acclimate to salinity changes more effectively.

Lindahl & Runnström (1929) showed that *Psammechinus miliaris* from the littoral (Z form) and sublittoral (S form) had different salinity optima. Gezelius (1963) reported the littoral growth form

had an optimal salinity range of 20-32 ppt, whereas the sub-littoral growth form 26-38 ppt. Mature examples of the littoral growth form tolerated 15 ppt for a period of 27 days however were not able to produce gametes at this salinity.

Davenport & Kjørsvik (1982) reported the presence of large horse mussels in rock pools at 16 psu in Norway, subject to freshwater inflow, and noted that they were probably exposed to lower salinities. By keeping the shell valves closed the fluid in the mantle cavity of two individuals was found to be at a salinity of 28–29 despite some hours of exposure (Davenport & Kjørsvik, 1982). Short-term tolerances to a salinity of 15 were similarly identified for Modiolus modiolus from the White Sea, north west Russia (where salinity is typically 25), whereas salinity levels of between 30 and 35 appeared optimal. However, after a winter and spring of extremely high rainfall, populations of Modiolus modiolus at the entrance to Loch Leven (near Fort William) were found dead, almost certainly due to low salinity outflow (K. Hiscock, pers. comm). Holt et al. (1998) reported that dense populations of very young Modiolus modiolus do occasionally seem to occur sub tidally in estuaries, but the species is more poorly adapted to fluctuating salinity than many other mussel species (Bayne, 1976) and dense populations of adults are not found in low salinity areas.

Laboratory experiments exposing Modiolus modiolus to reduced salinity water have demonstrated short-term effects. Pierce (1970) exposed Modiolus spp. to a range of salinities between 1.5 and 54 psu and reported that Modiolus modiolus survived for 21 days (the duration of the experiment) between 27 and 41 psu. Shumway (1977) exposed individual Modiolus modiolus to simulated tidal, (sinusoidal) fluctuations between full seawater (salinity 32‰) and 50% freshwater and to more abrupt changes in salinity in laboratory experiments. Individual Modiolus modiolus that were able to close their valves survived 10 days exposure to salinity changes compared with individuals which had their shells wedged open that survived for 3 days of the experiment only. Exposure to reduced salinities has been observed to lead to reduced ctenidial ciliary stroke, (after 3 days at a salinity of 15 and 10°C, Schlieper et al., 1958) and increased intracellular liquid/water (Gainey, 1994).

Sensitivity assessment. SS.SMp.KSwSS.SlatMxVS is found in both full and variable salinity, this assessment assumes a decrease to reduced salinity (18-30‰). Such a decrease in salinity may cause a decline in Saccharina latissima sporophyte growth and negatively affect Psammechinus miliaris reproduction. The available evidence indicates that Modiolus modiolus is an osmoconformer able to tolerate decreases in salinity for a short period. However, a decrease in salinity at the pressure benchmark from full salinity or variable to reduced (18-30 ppt) would be considered to result in the mortality of the characterizing species within the biotope over the course of a year. Resistance has been assessed 'Low'. Resilience has been assessed as 'Medium'. Sensitivity has been assessed as 'Medium'.

Water flow (tidal current) changes (local)

High

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

High

Not sensitive

Q: Medium A: High C: High

SS.SMp.KSwSS.SlatMxVS is found from strong (1.5-3 m/sec) -very weak (negligible) tidal streams (Connor et al., 2004). Indicating the characterizing species are tolerant of tidal streams within this range.

Peteiro & Freire (2013) measured Saccharina latissima growth from 2 sites, the first had maximal water velocities of 0.3m/sec and the second 0.1m/sec. At site 1 Saccharina latissima had significantly larger biomass than at site 2 (16 kg/m to 12 kg/m respectively). Peteiro & Freire (2013) suggested that faster water velocities were beneficial to Saccharina latissima growth.

However, Gerard & Mann (1979) found Saccharina latissima productivity is reduced in moderately strong tidal streams (≤ 1 m/sec) when compared to weak tidal streams (<0.5 m/sec). Despite the results published in Gerard & Mann (1979) Saccharina latissima can characterize or be a dominant in the tide swept biotopes IR.MIR.KT.XKTX & IR.MIR.KT.SlatT, which have been recorded from very strong (>3 m/sec) to moderately strong tidal streams (≤ 1 m/sec) (Connor *et al.*, 2004), indicating Saccharina latissima can tolerate greater tidal streams than <1 m/sec.

Holt et al. (1998) suggested water movement was important in the development of dense reefs and beds of Modiolus modiolus. It is likely therefore that there is an optimum range of water flows, currently unknown, which are strong enough to disperse larvae and provide food but are not so strong that the current removes the bed, prevents settlement of larvae within beds (which is key for self-recruiting populations) or prevents the extension of feeding siphons. Conversely, decreased flow rates may inhibit larval settlement and the supply of suspended food and allow greater siltation on beds.

Adult Modiolus modiolus occur commonly in areas with moderate to high water exchange in Nova Scotia (Wildish & Peer, 1983; Wildish & Kristmanson, 1985, 1994; Wildish & Fader, 1998; Wildish et al., 1998), and low field densities have been correlated with low current regimes and reduced food availability. Densities of up to 220 individuals/m2 have been recorded from the Faroese shelf (Dinesen, 1999) where maximal tidal current speed has been estimated to be between 79 and 98 cm/s at two Modiolus modiolus sites (Nørrevang et al., 1994: BIOFAR Stn. 661 & 662, cited from Dinesen & Morton, 2014). Mair et al. (2000) also observed that in Scottish sites with Modiolus modiolus beds, densities were greater where there were high tidal currents.

Sensitivity assessment. Large scale changes tidal velocities (>1m/sec) may influence biotope structure. However, the available evidence suggests that a change in flow velocities of between 0.1-0.2m/sec would not have a significant effect. Resistance has been assessed as 'High', resilience as 'High'. Sensitivity has been assessed as 'Not Sensitive' at the benchmark level.

Emergence regime changes



Medium Q: High A: Low C: High Medium

Q: Low A: Low C: Low

SS.SMp.KSwSS.SlatMxVS is recorded from the low shore to 20 m BCD An increase in emergence will result in an increased risk of desiccation and mortality of Saccharina latissima and Modiolus modiolus. Removal of canopy forming kelps, through desiccation, has also been shown to increase desiccation and mortality of understory macro-algae (Hawkins & Harkin, 1985). Providing that suitable substrata are present, the biotope is likely to re-establish further down the shore within a similar emergence regime to that which existed previously.

Sensitivity assessment. Resilience has been assessed as 'Low'. Resistance as 'Medium'. The sensitivity of this biotope to a change in emergence is considered as '**Medium**'.

(local)

Wave exposure changes High Q: Low A: NR C: NR

High Q: High A: High C: High

Not sensitive Q: Low A: Low C: Low

At the time of writing there is limited direct evidence for the effect of increases in wave exposure on Saccharina latissima or Psammechinus miliaris other than they are predominantly recorded in wave sheltered locations (Birkett et al., 1998; Kelly, 2000). Similarly there was no direct evidence for the effect of increased wave exposure on Modiolus modiolus. However, Modiolus modiolus is

recorded from moderately exposed-very sheltered locations (MNCR data see below). Due to their size (adults: 10-22 cm (Tyler-Walters, 2007) may become dislodged if wave action increases above this range within shallow examples of SS.SMp.KSwSS.SlatMxVS. Furthermore an increase in wave action may also remove smaller sediment fractions and therefore affect the biological community.

SS.SMp.KSwSS.SlatMxVS is recorded from sheltered-ultra wave sheltered sites (Connor *et al.*, 2004). Therefore, a large increase in wave exposure to e.g. moderate wave exposure is likely to have a fundamental effect on local sediment and characterizing species. However a change in nearshore significant wave height >3% but <5% is not likely to have a significant effect.

Sensitivity assessment. Wave exposure is one of the principal defining features biotope structures, and large changes in wave exposure are likely to alter the relative abundance of the dominant macro-algae, grazing and understory community, alter the sedimentary substratum and hence, the biotope. However a change in near shore significant wave height of 3-5% is unlikely to have any significant effect on SS.SMp.KSwSS.SlatMxVS. Resistance has been assessed as '**High**', resilience as '**High**' and sensitivity as '**Not Sensitive**' at the benchmark level.

Please note the latest version of the JNCC National Biodiversity Database was used as the source of the MNCR data. However, it should be noted that a) not all biotopes were recorded with full habitat/site information, and b) the extraction only recorded the habitat conditions where the biotope was recorded and not the relevant species presence, abundance or biomass within each site. Therefore, this information represents the range of habitat conditions in which the biotopes can be found rather than identifying optimum habitats for species. This caveat applies to all assessments made using this data.

A Chemical Pressures

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

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

Bryan (1984) suggested that the general order for heavy metal toxicity in seaweeds is: Organic Hg > inorganic Hg > Cu > Ag > Zn > Cd > Pb. Cole *et al*, (1999) reported that Hg was very toxic to macrophytes. The effects of copper, zinc and mercury on *Saccharina latissima* have been investigated by Thompson & Burrows (1984). They observed that the growth of sporophytes was significantly inhibited at 50 μ g Cu /l, 1000 μ g Zn/l and 50 μ g Hg/l. Zoospores were found to be more intolerant and significant reductions in survival rates were observed at 25 μ g Cu/l, 1000 μ g Zn/l and 5 μ g/l.

At the time of writing, little is known about the effects of heavy metals on echinoderms. Bryan (1984) reported that early work had shown that echinoderm larvae were intolerant of heavy metals, e.g. the intolerance of larvae of *Paracentrotus lividus* to copper (Cu) had been used to develop a water quality assessment. Kinne (1984) reported developmental disturbances in *Echinus esculentus* exposed to waters containing $25 \mu g / l$ of copper (Cu). Sea-urchins, especially the eggs and larvae, are used for toxicity testing and environmental monitoring (reviewed by Dinnel et al. 1988). Taken together with the findings of Gomez & Miguez-Rodriguez (1999) above it is likely

that echinoderms are intolerant of heavy metal contamination.

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.

Saccharina latissima fronds, being predominantly subtidal, would not come into contact with freshly released oil but only to sinking emulsified oil and oil adsorbed onto particles (Birkett *et al.*, 1998). The mucilaginous slime layer coating of laminarians may protect them from smothering by oil. Hydrocarbons in solution reduce photosynthesis and may be algicidal. However, Holt *et al.* (1995) reported that oil spills in the USA and from the '*Torrey Canyon*' had little effect on kelp forests. Similarly, surveys of subtidal communities at a number sites between 1-22.5m below chart datum showed no noticeable impacts of the Sea Empress oil spill and clean up (Rostron & Bunker, 1997). An assessment of holdfast fauna in *Laminaria* showed that although species richness and diversity decreased with increasing proximity to the *Sea Empress* oil spill, overall the holdfasts contained a reasonably rich and diverse fauna, even though oil was present in most samples (Sommerfield & Warwick, 1999).

Echinoderms seem especially sensitive to the toxic effects of oil, likely because of the large amount of exposed epidermis (Suchanek, 1993). Schäfer & Köhler (2009) found 20 day exposure to sublethal concentrations of phenanthrene resulted in severe ovarian lesions of *Psammechinus miliaris* limiting the production of gametes.

Following the Torrey Canyon incident, large numbers of dead *Psammechinus miliaris* were found in the vicinity of Sennen, UK possibly due to exposure to the oil spill and the heavy spraying of hydrocarbon based dispersants in that area (Smith, 1968). Other significant effects have been observed in other species of urchins. For example, mass mortality of the echinoderm *Echinocardium cordatum* was observed shortly after the Amoco Cadiz oil spill (Cabioch et al., 1978) and reduced abundance of the species was detectable up to >1000m away one year after the discharge of oil-contaminated drill cuttings in the North Sea (Daan & Mulder, 1996). In the Mediterranean around Naples, urchins were absent from areas which has visible signs of massive pollution of both sewage and oil. *Echinus esculentus* populations in the vicinity of an oil terminal in A Coruna Bay, Spain, showed developmental abnormalities in the skeleton. The tissues contained high levels of aliphatic hydrocarbons, naphthalenes, pesticides and heavy metals (Zn, Hg, Cd, Pb, and Cu) (Gomez & Miguez-Rodriguez 1999). But the observed effects may have been due to a single contaminant or synergistic effects of all present.

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

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

Johansson (2009) exposed samples of *Saccharina latissima* to several antifouing compounds, observing chlorothalonil, DCOIT, dichlofluanid and tolylfluanid inhibited photosynthesis. Exposure to Chlorothalonil and tolylfluanid, was also found to continue inhibiting oxygen evolution after exposure had finished, and may cause irreversible damage.

Smith (1968) noted that epiphytic and benthic red algae were intolerant of dispersant or oil

contamination due to the Torrey Canyon oil spill; only the epiphytes *Crytopleura ramosa* and *Spermothamnion repens* and some tufts of *Jania rubens* survived together with *Osmundea pinnatifida*, *Gigartina pistillata* and *Phyllophora crispa* from the sublittoral fringe.

Considerable observations and work, mainly on *Echinus esculentus* but also on *Psammechinus miliaris* (Smith, 1968; Gomez & Miguez-Rodriguez, 1999; Dinnel et al., 1988) indicate high intolerance to synthetic contaminants. Newton & McKenzie (1995) state that echinoderms tend to be very intolerant of various types of marine pollution, but there is little more detailed information than this. Following the Torrey Canyon incident, large numbers of dead *Psammechinus miliaris* in the vicinity of Sennen, UK presumably due to the heavy spraying of dispersants in that area and exposure to the oil spill (Smith, 1968).

Radionuclide contamination	Not relevant (NR)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	q: NR A: NR C: NR
No evidence			
Introduction of other substances	Not Assessed (NA)	Not assessed (NA)	Not assessed (NA)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR
This pressure is Not a	assessed.		
De-oxygenation	<mark>Medium</mark>	<mark>High</mark>	<mark>Low</mark>
	Q: Medium A: High C: High	Q: Medium A: High C: High	Q: Medium A: High C: High

Reduced oxygen concentrations can inhibit both photosynthesis and respiration in macroalgae (Kinne, 1977). Despite this, macroalgae are thought to buffer the environmental conditions of low oxygen, thereby acting as a refuge for organisms in oxygen depleted regions especially if the oxygen depletion is short-term (Frieder *et al.*, 2012). A rapid recovery from a state of low oxygen is expected if the environmental conditions are transient. If levels do drop below 4 mg/l negative effects on these organisms can be expected with adverse effects occurring below 2mg/l (Cole *et al.*, 1999).

Theede *et al.* (1969) examined the relative tolerance of gill tissue from several species of bivalve to exposure to 0.21 mg/l O_2 with or without 6.67 mg of sulphide (at 10 °C and 30 psu). *Modiolus modiolus* tissue was found to be the most resistant of the species studied, retaining some ciliary activity after 120 hrs compared with 48 hrs for *Mytilus edulis*.

Under hypoxic conditions echinoderms become less mobile and stop feeding. Death of a bloom of the phytoplankton *Gyrodinium aureolum* in Mounts Bay, Penzance in 1978 produced a layer of brown slime on the sea bottom. This resulted in the death of fish and invertebrates, including *Echinus esculentus*, presumably due to anoxia caused by the decay of the dead dinoflagellates (Griffiths *et al.*, 1979). Spicer (1995) investigated the effects of environmental hypoxia on the oxygen and acid-base status of *Psammechinus miliaris*. Oxygen uptake is not regulated by this species during progressive hypoxia. The habitat of this species includes rock pools on the shore that can experience quite severe hypoxia or even anoxia. *Psammechinus miliaris* must be able to tolerate low oxygen conditions provided the event is brief. In prolonged events,

subtidal *Psammechinus miliaris* would presumably react in a similar fashion to the *Echinus* esculentus above.

Sensitivity Assessment. Reduced oxygen levels are likely to inhibit macroalgal photosynthesis and respiration but not cause a loss of the macroalgae population directly. Resistance has been assessed as '**Medium**', Resilience as '**High**'. Sensitivity has been assessed as '**Low**' at the benchmark level.

Nutrient enrichment

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

Not sensitive Q: NR A: NR C: NR

Johnston & Roberts (2009) conducted a meta analysis, which reviewed 216 papers to assess how a variety of contaminants (including sewage and nutrient loading) affected 6 marine habitats (including subtidal reefs). A 30-50% reduction in species diversity and richness was identified from all habitats exposed to the contaminant types. Johnston & Roberts (2009) however also highlighted that macroalgal communities are relative tolerant to contamination, but that contaminated communities can have low diversity assemblages which are dominated by opportunistic and fast growing species (Johnston & Roberts, 2009 and references therein).

Conolly & Drew (1985) found *Saccharina latissima* sporophytes had relatively higher growth rates when in close proximity to a sewage outlet in St Andrews, UK when compared to other sites along the east coast of Scotland. At St Andrews nitrate levels were 20.22 μ M, which represents an approx 25% increase when compared to other comparable sites (approx 15.87 μ M). Handå et al. (2013) also reported *Saccharina latissima* sporophytes grew approx 1% faster per day when in close proximity to Norwegian Salmon farms, where elevated ammonium can be readily absorbed. Read *et al.* (1983) reported after the installation of a new sewage treatment works which reduced the suspended solid content of liquid effluent by 60% in the Firth of Forth, *Saccharina latissima* became abundant where previously it had been absent.

Navarro & Thompson (1996) suggested that *Modiolus modiolus* was adapted to an intermittent and often inadequate food supply. The persistence of a *Modiolus modiolus* population in the vicinity of a sewage sludge dumping site, North Norfolk (Richardson et al., 2001) suggests that the species is tolerant of high nutrient levels. Moderate nutrient enrichment may, therefore, be beneficial by increasing phytoplankton productivity and organic particulates, and hence food availability.

Sensitivity assessment. The evidence suggests that enrichment would not directly affect *Saccharina latissima* and may benefit *Modiolus modiolus*. Nutrient enrichment may increase turbidity which may decrease water clarity (see above) and therefore macroalgae photosynthesis. But This biotope has been assessed as **'Not sensitive**' at the pressure benchmark, that assumes compliance with good status as defined by the WFD.

Organic enrichment

Medium

Q: High A: High C: High

High Q: High A: High C: High



Johnston & Roberts (2009) conducted a meta analysis, which reviewed 216 papers to assess how a variety of contaminants (including sewage and nutrient loading) affected 6 marine habitats (including subtidal reefs). A 30-50% reduction in species diversity and richness was identified from

all habitats exposed to the contaminant types. Johnston & Roberts (2009) however also highlighted that macroalgal communities are relative tolerant to contamination, but that contaminated communities can have low diversity assemblages which are dominated by opportunistic and fast growing species (Johnston & Roberts, 2009 and references therein).

The persistence of a *Modiolus modiolus* population in the vicinity of a sewage sludge dumping site, North Norfolk (Richardson et al., 2001) suggests that the species is tolerant of high levels of organic matter. At the pressure benchmark which refers to enrichment rather than gross organic pollution (Tillin & Tyler-Walters, 2014) the extra rate of organic matter accumulation may not far exceed the natural background level, particularly in sheltered areas.

Sensitivity assessment. The evidence suggests that enrichment would not directly affect the characterizing species but that the community may suffer an overall reduction in species richness (Johnston & Roberts, 2009). In addition, organic enrichment may increase turbidity which may decrease water clarity and therefore macro-algae photosynthesis (see water clarity above). Resistance has therefore been assessed as '**Medium**', resilience as '**High**', and sensitivity has been assessed as '**Low**'.

A Physical Pressures

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

<mark>None</mark> Q: High A: High C: High Very Low Q: High A: High C: High

Q: High A: High C: High

High

If sediment were replaced with rock or artificial substrata, this would represent a fundamental change to the biotope (Macleod *et al.*, 2014). All the characterizing species within this biotope can grow in rock biotopes (Birkett *et al.*, 1998; Connor *et al.*, 2004), however SS.SMp.KSwSS is by definition a sediment biotope and introduction of rock would change it to a rock based biotope.

Sensitivity assessment. Resistance to the pressure is considered '**None**', and resilience '**Very low**'. Sensitivity has been assessed as '**High**'.

Physical change (to another sediment type)



Very Low Q: High A: High C: High



Q: High A: High C: High

The benchmark for this pressure refers to a change in one Folk class. The pressure benchmark originally developed by Tillin *et al.*, (2010) used the modified Folk triangle developed by Long (2006) which simplified sediment types into four categories: mud and sandy mud, sand and muddy sand, mixed sediments and coarse sediments. The change referred to is therefore a change in

sediment classification rather than a change in the finer-scale original Folk categories (Folk, 1954). The change in one Folk class is considered to relate to a change in classification to adjacent categories in the modified Folk triangle. For mixed sediments and sand and muddy sand habitats a change in one Folk class may refer to a change to any of the sediment categories. Dredging and dumping of sediment, and infrastructure developments, can lead to changes in sediment character.

SS.SMp.KSwSS.SlatMxVS occurs on mixed substrata, therefore within this pressure a change in one folk class relates to a change to either "Coarse sediment", "Mud and sandy Mud" and "Sand and sandy mud". Macro-algae are likely to successfully recruit onto the larger sediment/small rock fractions within these biotopes (e.g. gravel, pebbles, cobbles).Therefore, if the proportion of stabilised large sediment/small rock fractions increased this may benefit these biotopes. Conversely if the proportion of smaller sediment fractions increased within these biotopes (as with "Mud and sandy Mud" and "Sand and sandy mud") then macro-algal recruitment would likely be significantly reduced.

Sensitivity assessment. Resistance has been assessed as '**None**', resilience as **Very low** (the pressure is a permanent change), and sensitivity as **High.**

Habitat structure changes - removal of	None	Medium	Medium
	Q: High A: High C: High	Q: High A: High C: High	Q: High A: High C: High

SS.SMp.KSwSS.SlatMxVS is a sediment biotope, found on a varied mixture of sediment and rock fractions. Extraction of substratum to 30 cm is likely to remove small sediment fractions (e.g. gravel) and may mobilize the remaining larger rock fractions (e.g. cobbles) causing high mortality within the resident community.

Sensitivity assessment. Resistance has been assessed as '**None**', Resilience as '**Medium**'. Sensitivity has been assessed as '**Medium**'.

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

Q: High A: High C: High

Q: High A: High C: High

Medium

Abrasion of the substratum e.g. from bottom or pot fishing gear, cable laying etc. may cause localised mobility of the substrata and mortality of the resident community. The effect would be situation dependent however if bottom fishing gear were towed over a site it may mobilise a high proportion of the rock substrata and cause high mortality in the resident community e.g. overturning cobbles and causing mortality in the attached algal canopies.

No specific examples of anthropogenic abrasion could be found for this biotope. However, bottom fishing gear (e.g. scallop dredging) are known to cause high mortality in bycatch species by overturning sediment and physically crushing fragile species (Bradshaw *et al.*, 2001), which includes urchins.

The test of *Psammechinus miliaris* is brittle and easily damaged by impact or abrasion. Spines and podia may be damaged or broken off. The spines may provide some degree of cushioning for the test. Beam trawling was reported to remove ca 20 to 50% of this species (Kaiser & Spencer, 1994), and the impact of scallop dredging is likely to be similar. Damage to the test will generally be lethal,



if not outright because internal organs become exposed to predators and possible infection.

Sensitivity assessment. Resistance has been assessed as '**Low**', Resilience as '**Medium**'. Sensitivity has been assessed as '**Medium**'.

 Penetration or disturbance of the substratum subsurface
 None
 Medium

 Q: High A: High C: High
 Q: High A: High C: High
 Q: High A: High C: High

Penetration and/or disturbance of the substrate below the surface of the seabed, may cause localised mobility of the substrata and mortality of the resident community. No specific examples of anthropogenic penetration could be found for this biotope. However, bottom fishing gear (e.g. scallop dredging) are known to cause high mortality in bycatch species by overturning sediment and physically crushing fragile species (Bradshaw *et al.*, 2001), and may also cause high mortality in in-fauna species such as *Cerianthus lloydii*.

Sensitivity assessment. Resistance has been assessed as '**None**', Resilience as '**Medium**'. Sensitivity has been assessed as '**Medium**'.

Changes in suspended solids (water clarity)

<mark>None</mark> Q: High A: High C: High <mark>High</mark> Q: High A: High C: High Medium Q: High A: High C: High

Suspended Particle Matter (SPM) concentration has a linear relationship with sub surface light attenuation (Kd) (Devlin *et al.*, 1998). Light penetration influences the maximum depth at which kelp species can grow and it has been reported that laminarians grow at depths at which the light levels are reduced to 1 percent of incident light at the surface. Maximal depth distribution of laminarians therefore varies from 100 m in the Mediterranean to only 6-7 m in the silt laden German Bight. In Atlantic European waters, the depth limit is typically 35 m. In very turbid waters the depth at which kelp is found may be reduced, or in some cases excluded completely (e.g. Severn Estuary), because of the alteration in light attenuation by suspended sediment (Lüning, 1990; Birkett et al. 1998b). *Laminaria* spp. show a decrease of 50% photosynthetic activity when turbidity increases by 0.1/m (light attenuation coefficient =0.1-0.2/m; Staehr & Wernberg, 2009). An increase in water turbidity will likely affect the photosynthetic ability of kelp, decrease abundance and density.

Psammechinus miliaris is omnivorous, feeding directly on live and dead algae but also on an array of attached fauna (Kelly, 2000). The feeding plasticity of *Psammechinus miliaris* is likely to ameliorate some of the effects of diminished kelp growth as a result of decreased light availability.

Changes in light penetration or attenuation associated with this pressure are not relevant to *Modiolus modiolus*. However alterations in the availability of food or the energetic costs in obtaining food or changes in scour could either increase or decrease habitat suitability for *Modiolus modiolus*. *Modiolus modiolus* is found in a variety of turbid and clear water conditions (Holt *et al.*, 1998). Decreases in turbidity may increase phytoplankton productivity and potentially increase food availability. Therefore, *Modiolus modiolus* may benefit from reduced turbidity.

Sensitivity Assessment. A decrease in turbidity is likely to support enhanced growth (and possible

habitat expansion) and is therefore not considered in this assessment. Psammechinus miliaris and Modiolus modiolus are resilient to changes in water clarity. An increase in water clarity from clear to intermediate (10-100 mg/l) represent a change in light attenuation of ca 0.67-6.7 Kd/m, and is likely to result in a greater than 50% reduction in photosynthesis of Laminariales. Therefore, the dominant kelp species will probably suffer a severe decline and resistance to this pressure is assessed as 'None'. Resilience to this pressure is defined as 'High' at the benchmark level due to the scale of the impact. Hence, this biotope is regarded as having a sensitivity of 'Medium'.

Smothering and siltation Low rate changes (light)

Q: Low A: NR C: NR

High Q: High A: High C: High

Low Q: Low A: Low C: Low

Smothering by sediment e.g. 5 cm material during a discrete event, is unlikely to damage Saccharina latissima sporophytes but may affect holdfast fauna, gametophyte survival, interfere with zoospore settlement and therefore recruitment processes (Moy & Christie, 2012). Given the short life expectancy of Saccharina latissima (2-4 years (Parke, 1948)), SS.SMp.KSwSS.SlatMxVS is likely to be dependent on annual Saccharina latissima recruitment (Moy & Christie, 2012). Given the microscopic size of the gametophyte, 5 cm of sediment could be expected to significantly inhibit growth. However, laboratory studies showed that kelp gametophytes can survive in darkness for between 6-16 months at 8°C and would probably survive smothering by a discrete event. Once returned to normal conditions the gametophytes resumed growth or maturation within 1 month (Dieck, 1993). Intolerance to this factor is likely to be higher during the peak periods of sporulation and/or spore settlement.

Psammechinus miliaris is quite small (typically up to 4 cm) and is likely to be inundated by 5 cm of sediment (Jackson, 2008). If unable to 'dig out' of the sediment, deposited sediment may cause mortality. Mature individuals of Modiolus modiolus can reach 10-25 cm and are unlikely to completely inundated by light deposition of up to 5 cm during a discrete event.

SS.SMp.KSwSS.SlatMxVS is recorded from strong (1.5-3 m/sec) to very weak (negligible) tidal streams. Within tide swept examples of SS.SMp.KSwSS.SlatMxVS sediment are likely to be removed within a few tidal cycles. In tidally sheltered examples of SS.SMp.KSwSS.SlatMxVS sediments could remain and recovery rate would be related to sediment retention but will probably be dissipated within a year.

Sensitivity assessment. To reflect the potential effect that deposited sediment could have on Psammechinus miliaris. Resistance has been assessed as 'Low', resilience as 'High'. Sensitivity has been assessed as 'Low'.

Smothering and siltation None rate changes (heavy) Q: Low A: NR C: NR

High

Q: High A: High C: High

Medium

Q: Low A: Low C: Low

Smothering by sediment e.g. 30 cm material during a discrete event, is unlikely to damage Saccharina latissima sporophytes but will likely affect holdfast fauna, gametophyte survival, interfere with zoospore settlement and therefore recruitment processes (Moy & Christie, 2012). Given the short life expectancy of Saccharina latissima (2-4 years (Parke, 1948), SS.SMp.KSwSS.SlatMxVS is likely to be dependent on annual Saccharina latissima recruitment (Moy & Christie, 2012). Given the microscopic size of the gametophyte, 5 cm of sediment could be expected to significantly inhibit growth. However, laboratory studies showed that kelp gametophytes can survive in darkness for between 6-16 months at 8°C and would probably

survive smothering by a discrete event. Once returned to normal conditions the gametophytes resumed growth or maturation within 1 month (Dieck, 1993). Intolerance to this factor is likely to be higher during the peak periods of sporulation and/or spore settlement.

Psammechinus miliaris is quite small (typically up to 4 cm) and is likely to be inundated by 30 cm of sediment (Jackson, 2008). If unable to 'dig out' of the sediment, deposited sediment may cause mortality. Mature individuals of *Modiolus modiolus* can reach 10-25 cm and may also become inundated/smothered by heavy deposition of up to 30 cm during a discrete event.

SS.SMp.KSwSS.SlatMxVS is recorded from strong (1.5-3 m/sec) to very weak (Negligible) tidal streams. Within tide swept examples of SS.SMp.KSwSS.SlatMxVS sediment are likely to be removed within a few tidal cycles. In tidally sheltered examples of SS.SMp.KSwSS.SlatMxVS sediments could remain and recovery rate would be related to sediment retention but will probably be dissipated within a year.

Sensitivity assessment. To reflect the potential effect that deposited sediment could have on *Psammechinus miliaris* and *Modiolus modiolus*. Resistance has been assessed as '**None**', resilience as '**Medium**'. Sensitivity has been assessed as '**Medium**'.

Litter	Not Assessed (NA)	Not assessed (NA)	Not assessed (NA)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR
Not assessed. There is	s no evidence to suggest t	hat litter would significan	tly affect kelp.
Electromagnetic changes	Not relevant (NR)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	q: NR A: NR C: NR
No evidence			
Underwater noise	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
changes	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR
Not relevant			
Introduction of light or shading	Low	<mark>Medium</mark>	<mark>Medium</mark>
	Q: Low A: NR C: NR	Q: Low A: NR C: NR	Q: Low A: Low C: Low

There is no evidence to suggest that anthropogenic light sources would affect macroalgae. Shading (e.g. by construction of a pontoon, pier etc) could adversely affect SS.SMp.KSwSS.SlatMxVS in areas where the water clarity is also low, and tip the balance to shade tolerant species, resulting in the loss of *Saccharina latissima* from areas of the biotope directly within the shaded area, or a reduction in seaweed abundance.

Sensitivity assessment. Resistance is probably '**Low**', with a '**High**' resilience and a sensitivity of '**Low**', albeit with 'low' confidence due to the lack of direct evidence.

Barrier to species movement

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

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

Not relevant. This pressure is considered applicable to mobile species, e.g. fish and marine mammals rather than seabed habitats. Physical and hydrographic barriers may limit the dispersal of spores, but spore dispersal is not considered under the pressure definition and benchmark.

Death or injury by	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
collision	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Not relevant. Collision from grounding vessels is addressed under abrasion above.

 Visual disturbance
 Not relevant (NR)
 Not relevant (NR)
 Not relevant (NR)

 Q: NR A: NR C: NR
 Q: NR A: NR C: NR
 Q: NR A: NR C: NR
 Q: NR A: NR C: NR

Not relevant

Biological Pressures

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

Saccharina latissima has shown significant regional acclimation to environmental conditions. Gerard & Dubois (1988) found Saccharina latissima sporophytes which were regularly exposed to \geq 20°C could tolerate these high temperatures, whereas sporophytes from other populations which rarely experience \geq 17°C showed 100% mortality after 3 weeks of exposure to 20°C. It is therefore possible that transplanted eco-types of Saccharina latissima may react differently to environmental conditions that differ from those of their origin.

Modiolus modiolus bed restoration projects may translocate stock to re-populate areas of suitable habitat (Elsasser *et al.*, 2013). However, no evidence was found for detrimental effects arising from this practice, although there is potential for the movement of pathogens and non-indigenous, invasive species.

However, at the time of writing there is **No evidence** for translocation of any other characzerising species over significant geographic distances. Nor is there any evidence regarding the genetic modification or effects of translocation.

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

Very Low

High

Q: High A: High C: High

Q: High A: High C: High

Undaria pinnatifida has received a large amount of research attention as a major Invasive Non Indigenous Species (INIS) which could out-compete native UK kelp habitats (see Farrell & Fletcher, 2006; Thompson & Schiel, 2012, Brodie *et al.*, 2014; Hieser *et al.*, 2014). *Undaria pinnatifida* was first recorded in the UK, Hamble Estuary, in June 1994 (Fletcher & Manfredi, 1995) and has since spread to a number of British ports. *Undaria pinnatifida* is an annual species, sporophytes appear in Autumn and grow rapidly throughout winter and spring during which they can reach a length of 1.65m (Birkett *et al.*, 1998). Farrell & Fletcher (2006) suggested that native short lived species that occupy similar ecological niches to *Undaria pinnatifida*, such as *Saccharina latissima*, are likely to be worst affected and out-competed by *Undaria pinnatifida*. Where present an abundance of *Undaria pinnatifida* has corresponded to a decline in *Saccharina latisima* (Farrel & Fletcher, 2006) and *Laminaria hyperborea* (Hieser *et al.*, 2014).

In New Zealand, Thompson & Schiel (2012) observed that native fucoids could out-compete *Undaria pinnatifida* and re-dominate the substratum. However, Thompson & Schiel (2012) suggested the fucoid recovery was partially due to an annual *Undaria pinnatifida* die back, which as noted by Heiser *et al.*, (2014) does not occur in Plymouth sound, UK. *Undaria pinnatifida* was successfully eradicated on a sunken ship in Clatham Islands, New Zealand, by applying a heat treatment of 70°C (Wotton *et al.*, 2004) however numerous other eradication attempts have failed, and as noted by Fletcher & Farrell, (1999) once established *Undaria pinnatifida* resists most attempts of long-term removal. The biotope is unlikely to fully recover until *Undaria pinnatifida* is fully removed from the habitat, which as stated above is unlikely to occur.

At the time of writing, *Undaria pinnatifida* is not currently recorded in Scotland (NBN, 2015), where SS.SMp.KSwSS.SlatMxVS is isolated (Connor *et al.*, 2004). However, *Undaria pinnatifida* has a lower temperature threshold of 0°C and a reproductive boundary of <7°C (Sanderson, 1990). On the west coast of Scotland sea surface temperature ranges from 14.5-16.9°C in summer and 4-10°C in winter (Beszczynska-Möller & Dye, 2013). *Undaria pinnatifida* begins reproduction in spring-summer, and the winter temperature is not likely to go below the *Undaria pinnatifida*'s temperature tolerance. It therefore seems likely that *Undaria pinnatifida* would not be temperature limited in Scotland and could potentially colonize if introduced.

Sensitivity assessment. Therefore, where *Undaria pinnatifida* becomes established it could outcompete the characteristic kelp species, resulting in loss of the biotope. Resistance to the pressure is considered **'Low'**, and resilience **'Very Low'**. The sensitivity of this biotope to introduction of microbial pathogens is assessed as **'High'**.

Introduction of microbial Medium pathogens Q: Medium

Medium Q: Medium A: High C: Medium <mark>High</mark> Q: Low A: NR C: NR Low Q: Low A: Low C: Low

Saccharina latissima may be infected by the microscopic brown alga Streblonema aecidioides. Infected algae show symptoms of Streblonema disease, i.e. alterations of the blade and stipe ranging from dark spots to heavy deformations and completely crippled thalli (Peters & Scaffelke, 1996). Infection can reduce growth rates of host algae.

Psammechinus miliaris is susceptible to 'Bald-sea-urchin disease', which causes lesions, loss of spines, tube feet, pedicellariae, destruction of the upper layer of skeletal tissue and death (Maes et al., 1986). It is thought to be caused by the bacteria Vibrio anguillarum and Aeromonas salmonicida. This disease has been recorded from *Psammechinus miliaris* from the French Atlantic coast. Although associated with mass mortalities of *Strongylocentrotus franciscanus* in California and *Paracentrotus lividus* in the French Mediterranean there is no evidence of mass mortalities of *Psammechinus miliaris* associated with this disease around Britain and Ireland.

Brown & Seed (1977) reported a low level of infestation (ca 2%) of Modiolus modiolus with pea

crabs *Pinnotheres* sp. in Port Erin, Isle of Man and Strangford Lough. Comely (1978) reported that ca 20% of older specimens, in an ageing population, were damaged or shells malformed by the boring sponge *Cliona celata*. Infestation by the boring sponge reduces the strength of the shell and may render the population more intolerant of physical disturbance (see above). However, little other information concerning the effects of parasites or disease on the condition of horse mussels was found.

Shumway (1990) reviewed the effects of algal blooms on shellfish and reported that a bloom of *Gonyaulax tamarensis (Protogonyaulax)* was highly toxic to *Modiolus modiolus*. Shumway (1990) also noted that both *Mytilus spp*. and *Modiolus spp*. accumulated paralytic shellfish poisoning (PSP) toxins faster than most other species of shellfish, e.g. horse mussels retained *Gonyaulax tamarensis* toxins for up to 60 days (depending on the initial level of contamination). Landsberg (1996) also suggested that there was a correlation between the incidence of neoplasia or tumours in bivalves and out-breaks of paralytic shellfish poisoning in which bivalves accumulate toxins from algal blooms, although a direct causal effect required further research.

The parasites *Martelia refringens* or other *Martelia sp.* can cause significant bivalve infections. Although these have been reported to infect *Modiolus modiolus* (Bower et al., 2004) no evidence was available to assess the scale of impact and therefore there is not enough evidence to assess sensitivity of *Modiolus modiolus* to this pressure

Sensitivity assessment. Evidence suggests that a number of characterizing species are susceptible to a number of disease or parasites that could result in loss of condition and possibly a proportion of the individual species populations. Therefore, resistance to the pressure is considered '**Medium**', and resilience '**High**'. The sensitivity of this biotope to introduction of microbial pathogens is assessed as '**Low'**.

Removal of target	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
species	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Targeted removal of characterizing species SS.SMp.KSwSS.SlatMxVS would likely have a fundamental effect on the ecology. *Saccharina latissima* is commercially cultivated, however typically sporophytes are matured on ropes (Handå et al 2013) and not directly extracted from the seabed, as is the case with *Laminaria hyperborea* (see Christie *et al.*, 1998). As a consequence related literature on which to assess the "resistance" of *Saccharina latissima* to targeted harvesting is sparse. *Psammechinus miliaris* is targeted as a potential aquaculture species. When fed a nutritious diet in culture, the gonad biomass rapidly proliferates which can then be marketed as urchin "roe" (Kelly et al., 1998; 2000). However, a study of a littoral and sublittoral population, Kelly (2000) concluded that a wild fishery was not commercially viable because of the low gonad content of wild populations. While some extraction of *Psammechinus miliaris* may conceivably develop for roe-enhancement through feeding artificial or nutrient enriched diets (Dr Maeve Kelly pers comm.), this is currently not in practice within the UK.

Artisanal fisheries have targeted *Modiolus modiolus* as bait for the long-ling fishery (Jeffreys 1863; Wiborg 1946) and, more locally, for human consumption around the British Isles (Jeffreys 1863; Holt et al. 1998) and the Faroe Islands (Dinesen & Ockelmann 2005). However at the time of writing *Modiolus modiolus* is not directly targeted in the UK.

Sensitivity assessment. At the time of writing none of the characterizing species are commercially extracted from the seabed. If extracted in the future resistance would need to be re-assessed. This

pressure has been assessed as 'Not Relevant.

Removal of non-target species



Q: High A: High C: High



Q: High A: High C: High



Q: High A: High C: High

Incidental removal of characterizing species from this biotope would likely have a fundamental effect on the ecology. *Saccharina latissima* is commercially cultivated, however typically sporophytes are matured on ropes (Handå et al 2013) and not directly extracted from the seabed, as is the case with *Laminaria hyperborea* (see Christie *et al.*, 1998). As a consequence related literature on which to assess the "resistance" of *Saccharina latissima* to incidental harvesting is sparse.

Psammechinus miliaris may suffer as a result of trawling or dredging for other benthic species. Species with fragile tests such as urchins have been reported to be particularly sensitive to damage from mobile fishing gear (see Jennings & Kaiser, 1998; Bergman & van Santbrink, 2000). Kaiser & Spencer (1994) reported a ca20 - 50% mortality in *Psammechinus miliaris* as a result of a single pass of an experimental 4m beam trawl. Similarly, sparse *Modiolus modiolus* may be removed by a passing mobile gear, or crushed by mobilized cobbles and pebbles.

Sensitivity assessment. For this assessment it has been assumed that incidental removal could result in removal of the characterizing species, depending on the footprint of the activity. i. Resistance has been assessed as '**Low**', resilience as '**Medium**' and sensitivity as '**Medium**'.

Bibliography

Davenport J, Kjøsvik E. 1982. Observations on a Norwegian intertidal population of the horse mussel Modiolus modiolus (L.). *Journal of Molluscan Studies* 48: 370-1.

Allain, J-Y. 1978. Age et croissance de *Paracentrotus lividus* (Lamarck) et de *Psammechinus miliaris* (Gmelin) des côtes nord de Bretagne (Echinoidea). *Cahiers de Biologie Marine*, **19**, 11-21.

Andersen, G.S., Steen, H., Christie, H., Fredriksen, S. & Moy, F.E., 2011. Seasonal patterns of sporophyte growth, fertility, fouling, and mortality of *Saccharina latissima* in Skagerrak, Norway: implications for forest recovery. *Journal of Marine Biology*, **2011**, Article ID 690375, 8 pages.

Anwar, N.A., Richardson, C.A. & Seed, R., 1990. Age determination, growth rate, and population structure of the horse mussel *Modiolus modiolus. Journal of the Marine Biological Association of the United Kingdom*, **70**, 441-457.

Bayne, B.L., Widdows, J. & Thompson, R.J., 1976. Physiological integrations. In *Marine mussels: their ecology and physiology* (ed. B.L. Bayne), pp. 261-299. Cambridge: Cambridge University Press. [International Biological Programme 10.]

Bekkby, T. & Moy, F.E., 2011. Developing spatial models of sugar kelp (*Saccharina latissima*) potential distribution under natural conditions and areas of its disappearance in Skagerrak. *Estuarine Coastal and Shelf Science*, **95** (4), 477-483.

Bergman, M.J.N. & Van Santbrink, J.W., 2000b. Fishing mortality of populations of megafauna in sandy sediments. In *The effects of fishing on non-target species and habitats* (ed. M.J. Kaiser & S.J de Groot), 49-68. Oxford: Blackwell Science.

Beszczynska-Möller, A., & Dye, S.R., 2013. ICES Report on Ocean Climate 2012. In ICES Cooperative Research Report, vol. 321 pp. 73.

Birkett, D.A., Maggs, C.A., Dring, M.J. & Boaden, P.J.S., 1998b. Infralittoral reef biotopes with kelp species: an overview of dynamic and sensitivity characteristics for conservation management of marine SACs. *Natura 2000 report prepared by Scottish Association of Marine Science (SAMS) for the UK Marine SACs Project.*, Scottish Association for Marine Science. (UK Marine SACs Project, vol V.). Available from: http://www.ukmarinesac.org.uk/publications.htm

Bolton, J.J. & Lüning, K.A.F., 1982. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Marine Biology*, **66**, 89-94.

Bower, S.M., 1996. Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish: Bald-sea-urchin Disease. [On-line]. Fisheries and Oceans Canada. [cited 26/01/16]. Available from:

http://www.dfo-mpo.gc.ca/science/aah-saa/diseases-maladies/bsudsu-eng.html

Bower, S.M., 2004. Rickettsia-like and Chlamydia-like Organisms of Mussels. Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish.

http://www.pac.dfo-mpo.gc.ca/science/species-especes/shellfish-coquillages/diseases-maladies/pages/rcomu-eng.htm

Brodie J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M., Steinke, M., Yesson, C. & Anderson, K.M., 2014. The future of the northeast Atlantic benthic flora in a high CO₂ world. *Ecology and Evolution*, **4** (13), 2787-2798.

Brown, R.A. & R. Seed., 1976. *Modiolus modiolus* (L.) - an autoecological study. In *Proceedings of the 11th European Symposium on Marine Biology, Galway, 5-11 October, 1976. Biology of Benthic Organisms* (ed. B.F. Keegan, P.O. Ceidigh & Boaden, P.J.S.), pp. 93-100.

Brown, R.A., 1984. Geographical variation in the reproduction of the horse mussel, *Modiolus modiolus* (Mollusca: Bivalvia). *Journal of the Marine Biological Association of the United Kingdom*, **64**, 751-770.

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, M.T., Smale, D., O'Connor, N., Rein, H.V. & Moore, P., 2014. Marine Strategy Framework Directive Indicators for UK Kelp Habitats Part 1: Developing proposals for potential indicators. *Joint Nature Conservation Comittee*, Peterborough. Report no. 525.

Cabioch, L., Dauvin, J.C. & Gentil, F., 1978. Preliminary observations on pollution of the sea bed and disturbance of sub-littoral communities in northern Brittany by oil from the *Amoco Cadiz*. *Marine Pollution Bulletin*, **9**, 303-307.

Casas, G., Scrosati, R. & Piriz, M.L., 2004. The invasive kelp Undaria pinnatifida (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). *Biological Invasions*, **6** (4), 411-416.

Christie, H., Fredriksen, S. & Rinde, E., 1998. Regrowth of kelp and colonization of epiphyte and fauna community after kelp trawling at the coast of Norway. *Hydrobiologia*, **375/376**, 49-58.

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

Comely, C.A., 1978. Modiolus modiolus (L.) from the Scottish West coast. I. Biology. Ophelia, 17, 167-193.

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 1861075618. 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., Dalkin, M.J., Hill, T.O., Holt, R.H.F. & Sanderson, W.G., 1997a. Marine biotope classification for Britain and Ireland. Vol. 2. Sublittoral biotopes. *Joint Nature Conservation Committee*, *Peterborough, JNCC Report* no. 230, Version 97.06., *Joint Nature Conservation Committee*, Peterborough, JNCC Report no. 230, Version 97.06.

Conolly N.J. & Drew, E.A., 1985. Physiology of *Laminaria*. III. Effect of a coastal eutrophication on seasonal patterns of growth and tissue composition in *Laminaria digitata* and *L. saccharina*. *Marine Ecology*, *Pubblicazioni della Stazione Zoologica di Napoli I*, **6**, 181-195.

Daan, R. & Mulder, M., 1996. On the short-term and long-term impact of drilling activities in the Dutch sector of the North Sea *ICES Journal of Marine Science*, **53**, 1036-1044.

Dauvin, J.C., Bellan, G., Bellan-Santini, D., Castric, A., Francour, P., Gentil, F., Girard, A., Gofas, S., Mahe, C., Noel, P., & Reviers, B. de., 1994. Typologie des ZNIEFF-Mer. Liste des parametres et des biocoenoses des cotes francaises metropolitaines. 2nd ed. *Secretariat Faune-Flore, Museum National d'Histoire Naturelle, Paris (Collection Patrimoines Naturels, Serie Patrimoine Ecologique, No. 12).* Coll. Patrimoines Naturels, vol. 12, Secretariat Faune-Flore, Paris.

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

Dayton, P.K., Tegner, M.J., Parnell, P.E. & Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs*, **62**, 421-445.

de Schweinitz, E.H. & Lutz, R.A., 1976. Larval development of the northern Horse mussel, *Modiolus modiolus* (L.) including a comparison with the larvae of *Mytilus edulis* L. as an aid in planktonic identification. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, **150**, 348-360.

Devlin, M.J., Barry, J., Mills, D.K., Gowen, R.J., Foden, J., Sivyer, D. & Tett, P., 2008. Relationships between suspended particulate material, light attenuation and Secchi depth in UK marine waters. *Estuarine, Coastal and Shelf Science*, **79** (3), 429-439.

Dieck, T.I., 1992. North Pacific and North Atlantic digitate *Laminaria* species (Phaeophyta): hybridization experiments and temperature responses. *Phycologia*, **31**, 147-163.

Dieck, T.I., 1993. Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales: Phaeophyta) - ecological and biogeographical implications. *Marine Ecology Progress Series*, **100**, 253-264.

Dinesen, G.E., & Morton, B., 2014. Review of the functional morphology, biology and perturbation impacts on the boreal, habitatforming horse mussel *Modiolus modiolus* (Bivalvia: Mytilidae: Modiolinae). *Marine Biology Research*, **10** (9), 845-870.

Dinesen, G.E., Ockelmann, K.W. 2005. Spatial distribution and species distinction of *Modiolus modiolus* and syntopic Mytilidae (Bivalvia) in Faroese waters (NE Atlantic). BIOFAR Proceedings 2005. *Annales Societas Scientarium Færoenses* (Fróðskapparit), **41**, 125-136.

Dinnel, P.A., Pagano, G.G., & Oshido, P.S., 1988. A sea urchin test system for marine environmental monitoring. In *Echinoderm Biology. Proceedings of the Sixth International Echinoderm Conference, Victoria, 23-28 August 1987*, (R.D. Burke, P.V. Mladenov, P. Lambert, Parsley, R.L. ed.), pp 611-619. Rotterdam: A.A. Balkema.

Edwards, A., 1980. Ecological studies of the kelp *Laminaria hyperborea* and its associated fauna in south-west Ireland. *Ophelia*, **9**, 47-60.

Elmhirst, R., 1922. Notes on the breeding and growth of marine animals in the Clyde Sea area. *Report of the Scottish Marine Biological Association*, 19-43.

Elner, R.W. & Vadas, R.L., 1990. Inference in ecology: the sea urchin phenomenon in the northwest Atlantic. *American Naturalist*, **136**, 108-125.

Erwin, D.G., Picton, B.E., Connor, D.W., Howson, C.M., Gilleece, P. & Bogues, M.J., 1990. Inshore Marine Life of Northern Ireland. Report of a survey carried out by the diving team of the Botany and Zoology Department of the Ulster Museum in fulfilment of a contract with Conservation Branch of the Department of the Environment (N.I.)., Ulster Museum, Belfast: HMSO.

Farrell, P. & Fletcher, R., 2006. An investigation of dispersal of the introduced brown alga *Undaria pinnatifida* (Harvey) Suringar and its competition with some species on the man-made structures of Torquay Marina (Devon, UK). *Journal of Experimental Marine Biology and Ecology*, **334** (2), 236-243.

Fletcher, R.L. & Manfredi, C., 1995. The occurrence of *Undaria pinnatifida* (Phyaeophyceae, Laminariales) on the South Coast of England. *Botanica Marina*, **38** (4), 355-358.

Fletcher, R.L., 1996. The occurrence of 'green tides' - a review. In *Marine Benthic Vegetation*. *Recent changes and the Effects of Eutrophication* (ed. W. Schramm & P.H. Nienhuis). Berlin Heidelberg: Springer-Verlag. [Ecological Studies, vol. 123].

Fredriksen, S., Sjøtun, K., Lein, T.E. & Rueness, J., 1995. Spore dispersal in *Laminaria hyperborea* (Laminariales, Phaeophyceae). *Sarsia*, **80** (1), 47-53.

Frieder, C., Nam, S., Martz, T. & Levin, L., 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences*, **9** (10), 3917-3930.

Gerard, V.A. & Du Bois, K.R., 1988. Temperature ecotypes near the southern boundary of the kelp Laminaria saccharina. Marine Biology, **97**, 575-580.

Gerard, V.A. & Mann, K.H., 1979. Growth and production of Laminaria longicruris (Phaeophyta) populations exposed to different

intensities of water movement 1. Journal of Phycology, 15 (1), 33-41.

Gezelius, G., 1962. Adaptation of the sea urchin *Psammechinus miliaris* to different salinities. *Zoologiska Bidrag fran Uppsala*, **35**, 329-337.

Gommez, J.L.C. & Miguez-Rodriguez, L.J., 1999. Effects of oil pollution on skeleton and tissues of *Echinus esculentus* L. 1758 (Echinodermata, Echinoidea) in a population of A Coruna Bay, Galicia, Spain. In *Echinoderm Research* 1998. Proceedings of the Fifth *European Conference on Echinoderms*, *Milan*, 7-12 September 1998, (ed. M.D.C. Carnevali & F. Bonasoro) pp. 439-447. Rotterdam: A.A. Balkema.

Gorman, D., Bajjouk, T., Populus, J., Vasquez, M. & Ehrhold, A., 2013. Modeling kelp forest distribution and biomass along temperate rocky coastlines. *Marine Biology*, **160** (2), 309-325.

Hammer, L., 1972. Anaerobiosis in marine algae and marine phanerograms. In *Proceedings of the Seventh International Seaweed Symposium, Sapporo, Japan, August* 8-12, 1971 (ed. K. Nisizawa, S. Arasaki, Chihara, M., Hirose, H., Nakamura V., Tsuchiya, Y.), pp. 414-419. Tokyo: Tokyo University Press.

Handå, A., Forbord, S., Wang, X., Broch, O.J., Dahle, S.W., Storseth, T.R., Reitan, K.I., Olsen, Y. & Skjermo, J., 2013. Seasonal and depth-dependent growth of cultivated kelp (*Saccharina latissima*) in close proximity to salmon (*Salmo salar*) aquaculture in Norway. *Aquaculture*, **414**, 191-201.

Harkin, E., 1981. Fluctuations in epiphyte biomass following *Laminaria hyperborea* canopy removal. In *Proceedings of the Xth International Seaweed Symposium, Gø teborg, 11-15 August 1980* (ed. T. Levring), pp.303-308. Berlin: Walter de Gruyter.

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.

Hayward, P.J. 1988. Animals on seaweed. Richmond, Surrey: Richmond Publishing Co. Ltd. [Naturalists Handbooks 9].

Heiser, S., Hall-Spencer, J.M. & Hiscock, K., 2014. Assessing the extent of establishment of *Undaria pinnatifida* in Plymouth Sound Special Area of Conservation, UK. *Marine Biodiversity Records*, **7**, e93.

Henderson, J.T., 1929. Lethal temperatures of Lamellibranchiata. Contributions to Canadian Biology and Fisheries, 4, 395-412.

Hiscock, K. & Mitchell, R., 1980. The Description and Classification of Sublittoral Epibenthic Ecosystems. In The Shore Environment, Vol. 2, Ecosystems, (ed. J.H. Price, D.E.G. Irvine, & W.F. Farnham), 323-370. London and New York: Academic Press. [Systematics Association Special Volume no. 17(b)].

Hiscock, K., Southward, A., Tittley, I. & Hawkins, S., 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **14** (4), 333-362.

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.

Jasim, A.K.N. & Brand, A.R., 1989. Observations on the reproduction of Modiolus modiolus in the Isle of Man. Journal of the Marine Biological Association of the United Kingdom, **69**, 373-385.

Jasim, A.K.N., 1986. Some ecological aspects of Modiolus modiolus (L.) populations off the south-east of the Isle of Man., Ph.D. thesis, University of Liverpool.

Jeffreys, J.G., 1863. British conchology, or an account of the mollusca which now inhabit the British Isles and surrounding seas, vol. 1-5. London: John van Voorst.

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

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

JNCC, 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

Johnston, E.L. & Roberts, D.A., 2009. Contaminants reduce the richness and evenness of marine communities: a review and metaanalysis. *Environmental Pollution*, **157** (6), 1745-1752.

Jones, C.G., Lawton, J.H. & Shackak, M., 1994. Organisms as ecosystem engineers. Oikos, 69, 373-386.

Jones, D.J., 1971. Ecological studies on macro-invertebrate communities associated with polluted kelp forest in the North Sea. *Helgolander Wissenschaftliche Meersuntersuchungen*, **22**, 417-431.

Jones, L.A., Hiscock, K. & Connor, D.W., 2000. Marine habitat reviews. A summary of ecological requirements and sensitivity characteristics for the conservation and management of marine SACs. *Joint Nature Conservation Committee, Peterborough.* (UK *Marine SACs Project report.*). Available from: http://www.ukmarinesac.org.uk/pdfs/marine-habitats-review.pdf

Jones, N.S. & Kain, J.M., 1967. Subtidal algal recolonisation following removal of Echinus. Helgolander Wissenschaftliche Meeresuntersuchungen, **15**, 460-466.

Kain, J.M., 1964. Aspects of the biology of Laminaria hyperborea III. Survival and growth of gametophytes. Journal of the Marine

Biological Association of the United Kingdom, 44 (2), 415-433.

Kain, J.M. & Svendsen, P., 1969. A note on the behaviour of *Patina pellucida* in Britain and Norway. *Sarsia*, **38**, 25-30.

Kain, J.M., 1971a. Synopsis of biological data on Laminaria hyperborea. FAO Fisheries Synopsis, no. 87.

Kain, J.M., 1979. A view of the genus Laminaria. Oceanography and Marine Biology: an Annual Review, **17**, 101-161.

Kain, J.M., 1987. Photoperiod and temperature as triggers in the seasonality of *Delesseria sanguinea*. *Helgolander Meeresuntersuchungen*, **41**, 355-370.

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

Kain, J.M., Drew, E.A. & Jupp, B.P., 1975. Light and the ecology of Laminaria hyperborea II. In Proceedings of the Sixteenth Symposium of the British Ecological Society, 26-28 March 1974. Light as an Ecological Factor: II (ed. G.C. Evans, R. Bainbridge & O. Rackham), pp. 63-92. Oxford: Blackwell Scientific Publications.

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

Karsten, U., 2007. Research note: salinity tolerance of Arctic kelps from Spitsbergen. Phycological Research, 55 (4), 257-262.

Kelly, M.S., 2001. Environmental parameters controlling gametogenesis in the echinoid *Psammechinus miliaris*. Journal of *Experimental Marine Biology and Ecology*, **266**, 67-80.

Kelly, M.S., Brodie, C.C., & McKenzie, J.D., 1998. Somatic and gonadal growth of the sea urchin *Psammechinus miliaris* (Gmelin) maintained in polyculture with the Atlantic salmon. *Journal of Shellfish Research*, **17**, 1557-1562.

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

Kitching, J., 1941. Studies in sublittoral ecology III. *Laminaria* forest on the west coast of Scotland; a study of zonation in relation to wave action and illumination. *The Biological Bulletin*, **80** (3), 324-337

Kregting, L., Blight, A., Elsäßer, B. & Savidge, G., 2013. The influence of water motion on the growth rate of the kelp Laminaria hyperborea. Journal of Experimental Marine Biology and Ecology, **448**, 337-345.

Kruuk, H., Wansink, D. & Moorhouse, A., 1990. Feeding patches and diving success of otters, *Lutra lutra*, in Shetland. *Oikos*, **57**, 68-72.

Lüning, K., 1979. Growth strategy of three *Laminaria* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Hegloland (North Sea). *Marine Ecological Progress Series*, **1**, 195-207.

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

Lang, C. & Mann, K., 1976. Changes in sea urchin populations after the destruction of kelp beds. *Marine Biology*, **36** (4), 321-326.

Lein, T.E, Sjotun, K. & Wakili, S., 1991. Mass - occurrence of a brown filamentous endophyte in the lamina of the kelp *Laminaria hyperborea* (Gunnerus) Foslie along the south western coast of Norway *Sarsia*, **76**, 187-193.

Lindahl, P.E. & Runnström, J., 1929. Variation und Ökologie von Psammechinus miliaris (Gmelin). Acta Zoologica, 10, 401-484.

Lobban, C.S. & Harrison, P.J., 1997. Seaweed ecology and physiology. Cambridge: Cambridge University Press.

Lüning, K., 1990. Seaweeds: their environment, biogeography, and ecophysiology: John Wiley & Sons.

Lüning, K., 1980. Critical levels of light and temperature regulating the gametogenesis of three laminaria species (Phaeophyceae). *Journal of Phycology*, **16**, 1-15.

Müller, R., Laepple, T., Bartsch, I. & Wiencke, C., 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Botanica Marina*, **52** (6), 617-638.

Maes, P., Jangoux, M., & Fenaux, L., 1986. La maladie de l''oursin-chauve': Ultrastructure des lésions et charactérisation de leur pigmentation. Annales de l'Institut Océanographique. Nouvelle série, 62, 37-45.

Magorrian, B.H., Service, M., & Clarke, W., 1995. An acoustic bottom classification of Strangford Lough, Northern Ireland. *Journal of the Marine Biological Association of the United Kingdom*, **75**, 987-992.

Mair, J.M., Moore, C.G., Kingston, P.F. & Harries, D.B., 2000. A review of the status, ecology and conservation of horse mussel *Modiouls modiolus* beds in Scotland. *Scottish Natural Heritage Commissioned Report*. F99PA08.

Mann, K.H., 1982. Kelp, sea urchins, and predators: a review of strong interactions in rocky subtidal systems of eastern Canada, 1970-1980. *Netherlands Journal of Sea Research*, **16**, 414-423.

Miller III, H.L., Neale, P.J. & Dunton, K.H., 2009. Biological weighting functions for UV inhibiton of photosynthesis in the kelp *Laminaria hyperborea* (Phaeophyceae) 1. *Journal of Phycology*, **45** (3), 571-584.

Moore, P.G., 1973a. The kelp fauna of north east Britain I. Function of the physical environment. *Journal of Experimental Marine Biology and Ecology*, **13**, 97-125.

Moore, P.G., 1973b. The kelp fauna of north east Britain. II. Multivariate classification: turbidity as an ecological factor. *Journal of Experimental Marine Biology and Ecology*, **13**, 127-163.

Moore, P.G., 1978. Turbidity and kelp holdfast Amphipoda. I. Wales and S.W. England. *Journal of Experimental Marine Biology and Ecology*, **32**, 53-96.

Moore, P.G., 1985. Levels of heterogeneity and the amphipod fauna of kelp holdfasts. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis*, D.Sc. (ed. P.G. Moore & R. Seed), 274-289. London: Hodder & Stoughton Ltd.

Mortensen, T.H., 1927. Handbook of the echinoderms of the British Isles. London: Humphrey Milford, Oxford University Press.

Moy, F., Alve, E., Bogen, J., Christie, H., Green, N., Helland, A., Steen, H., Skarbøvik, E. & Stålnacke, P., 2006. Sugar Kelp Project: Status Report No 1. SFT Report TA-2193/2006, NIVA Report 5265 (in Norwegian, with English Abstract), 36 pp.

Moy, F.E. & Christie, H., 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Marine Biology Research*, **8** (4), 309-321.

Navarro, J.M. & Thompson, R.J., 1996. Physiological energetics of the horse mussel *Modiolus modiolus* in a cold ocean environment. *Marine Ecology Progress Series*, **138**, 135-148.

NBN, 2015. National Biodiversity Network 2015(20/05/2015). https://data.nbn.org.uk/

Newton, L.C. & McKenzie, J.D., 1995. Echinoderms and oil pollution: a potential stress assay using bacterial symbionts. *Marine Pollution Bulletin*, **31**, 453-456.

Nichols, D., 1981. The Cornish Sea-urchin Fishery. Cornish Studies, 9, 5-18.

Norderhaug, K., 2004. Use of red algae as hosts by kelp-associated amphipods. Marine Biology, 144 (2), 225-230.

Norderhaug, K.M. & Christie, H.C., 2009. Sea urchin grazing and kelp re-vegetation in the NE Atlantic. *Marine Biology Research*, **5** (6), 515-528.

Norderhaug, K.M., Christie, H. & Fredriksen, S., 2007. Is habitat size an important factor for faunal abundances on kelp (*Laminaria hyperborea*)? *Journal of Sea Research*, **58** (2), 120-124.

Nordheim, van, H., Andersen, O.N. & Thissen, J., 1996. Red lists of Biotopes, Flora and Fauna of the Trilateral Wadden Sea area, 1995. *Helgolander Meeresuntersuchungen*, **50** (Suppl.), 1-136.

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

Norton, T.A., Hiscock, K. & Kitching, J.A., 1977. The Ecology of Lough Ine XX. The Laminaria forest at Carrigathorna. Journal of Ecology, **65**, 919-941.

Parke, M., 1948. Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. Journal of the Marine Biological Association of the United Kingdom, **27**, 651-709.

Pedersen, M.F., Nejrup, L.B., Fredriksen, S., Christie, H. & Norderhaug, K.M., 2012. Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea*. *Marine Ecology Progress Series*, **451**, 45-60.

Penfold, R., Hughson, S., & Boyle, N., 1996. *The potential for a sea urchin fishery in Shetland*. http://www.nafc.ac.uk/publish/note5/note5.htm, 2000-04-14

Peteiro, C. & Freire, O., 2013. Biomass yield and morphological features of the seaweed Saccharina latissima cultivated at two different sites in a coastal bay in the Atlantic coast of Spain. *Journal of Applied Phycology*, **25**(1), 205-213.

Peters, A.F. & Schaffelke, B., 1996. *Streblonema* (Ectocarpales, Phaeophyceae) infection in the kelp *Laminaria saccharina* in the western Baltic. *Hydrobiologia*, **326/327**, 111-116.

Philippart, C.J., Anadón, R., Danovaro, R., Dippner, J.W., Drinkwater, K.F., Hawkins, S.J., Oguz, T., O'Sullivan, G. & Reid, P.C., 2011. Impacts of climate change on European marine ecosystems: observations, expectations and indicators. *Journal of Experimental Marine Biology and Ecology*, **400** (1), 52-69.

Pierce, S.K., 1970. The water balance of *Modiolus* (Mollusca: Bivalvia: Mytilidae): osmotic concentrations in changing salinities. *Comparative Biochemistry and Physiology*, **36**, 521-533.

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

Read, P.A., Anderson, K.J., Matthews, J.E., Watson, P.G., Halliday, M.C. & Shiells, G.M., 1983. Effects of pollution on the benthos of the Firth of Forth. *Marine Pollution Bulletin*, **14**, 12-16.

Richardson, C.A., Chensery, S.R.N. & Cook, J.M., 2001. Assessing the history of trace metal (Cu, Zn, Pb) contamination in the North Sea through laser ablation - ICP-MS of horse mussel *Modiolus modiolus* shells *Marine Ecology Progress Series*, **211**, 157-167.

Rinde, E. & Sjøtun, K., 2005. Demographic variation in the kelp *Laminaria hyperborea* along a latitudinal gradient. *Marine Biology*, **146** (6), 1051-1062.

Rostron, D.M. & Bunker, F. St P.D., 1997. An assessment of sublittoral epibenthic communities and species following the Sea Empress oil spill. A report to the Countryside Council for Wales from Marine Seen & Sub-Sea Survey., Countryside Council for Wales, Bangor, CCW Sea Empress Contact Science, no. 177.

Rowell, T.W., 1967. Some aspects of the ecology, growth and reproduction of the horse mussel Modiolus modiolus., MSc Thesis. Queens' University, Ontario

Schäfer, S. & Köhler, A., 2009. Gonadal lesions of female sea urchin (Psammechinus miliaris) after exposure to the polycyclic aromatic hydrocarbon phenanthrene. *Marine environmental research*, **68** (3), 128-136.

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.

Schlieper, E., Kowalski, R. & Erman, P., 1958. Beitrag zur öklogisch-zellphysiologishen Charakterisierung des borealen Lamellibranchier Modiolus modiolus L. *Kieler Meeresforsch*, **14**, 3-10.

SeaTemperature, 2015. World Sea Temperatures. (15/10/2015). http://www.seatemperature.org/

Seed, R. & Brown, R.A., 1977. A comparison of the reproductive cycles of *Modiolus modiolus* (L.), *Cerastoderma* (=*Cardium*) *edule* (L.), and *Mytilus edulis* L. in Strangford Lough, Northern Ireland. *Oecologia*, **30**, 173-188.

Seed, R. & Brown, R.A., 1978. Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *Journal of Animal Ecology*, **47**, 283-292.

Shumway, S.E., 1977. Effect of salinity fluctuations on the osmotic pressure and Na⁺, Ca²⁺ and Mg²⁺ ion concentrations in the hemolymph of bivalve molluscs. *Marine Biology*, **41**, 153-177.

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.

Sivertsen, K., 1997. Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2872-2887.

Sjøtun, K., Christie, H. & Helge Fosså, J., 2006. The combined effect of canopy shading and sea urchin grazing on recruitment in kelp forest (*Laminaria hyperborea*). *Marine Biology Research*, **2** (1), 24-32.

Sjøtun, K. & Schoschina, E.V., 2002. Gametophytic development of *Laminaria* spp. (Laminariales, Phaeophyta) at low temperatures. *Phycologia*, **41**, 147-152.

Sjøtun, K., Fredriksen, S., Lein, T.E., Runess, J. & Sivertsen, K., 1993. Population studies of *Laminaria hyperborea* from its northen range of distribution in Norway. *Hydrobiologia*, **260/261**, 215-221.

Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N. & Hawkins, S.J., 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecology and evolution*, **3** (11), 4016-4038.

Smale, D.A., Wernberg, T., Yunnie, A.L. & Vance, T., 2014. The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. *Marine ecology*.

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

Somerfield, P.J. & Warwick, R.M., 1999. Appraisal of environmental impact and recovery using *Laminaria* holdfast faunas. *Sea Empress*, *Environmental Evaluation Committee.*, *Countryside Council for Wales*, *Bangor*, *CCW Sea Empress Contract Science*, *Report* no. 321.

Staehr, P.A. & Wernberg, T., 2009. Physiological responses of *Ecklonia radiata* (Laminariales) to a latitudinal gradient in ocean temperature. *Journal of Phycology*, **45**, 91-99.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental conservation*, **29** (04), 436-459.

Steneck, R.S., Vavrinec, J. & Leland, A.V., 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems*, **7** (4), 323-332.

Suchanek, T.H., 1993. Oil impacts on marine invertebrate populations and communities. American Zoologist, 33, 510-523.

Theede, H., Ponat, A., Hiroki, K. & Schlieper, C., 1969. Studies on the resistance of marine bottom invertebrates to oxygendeficiency and hydrogen sulphide. *Marine Biology*, **2**, 325-337.

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

Thompson, R.S. & Burrows, E.M., 1984. The toxicity of copper, zinc and mercury to the brown macroalga *Laminaria saccharina*. In *Ecotoxicological testing for the marine environment* (ed. G. Persoone, E. Jaspers, & C. Claus), Vol. 2, pp. 259-269. Ghent: Laboratory for biological research in aquatic pollution, State University of Ghent.

Tillin, H. & Tyler-Walters, H., 2014. Assessing the sensitivity of subtidal sedimentary habitats to pressures associated with marine activities. Phase 2 Report – Literature review and sensitivity assessments for ecological groups for circalittoral and offshore Level 5 biotopes. *JNCC Report* No. 512B, 260 pp. Available from: www.marlin.ac.uk/publications

Ursin, E., 1960. A quantitative investigation of the echinoderm fauna of the central North Sea. *Meddelelser fra Danmark Fiskeri-og-Havundersogelser*, **2** (24), pp. 204.

Vadas, R.L. & Elner, R.W., 1992. Plant-animal interactions in the north-west Atlantic. In Plant-animal interactions in the marine benthos, (ed. D.M. John, S.J. Hawkins & J.H. Price), 33-60. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46].

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 den Hoek, C., 1982. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. *Biological Journal of the Linnean Society*, **18**, 81-144.

Vost, L.M., 1983. The influence of Echinus esculentus grazing on subtidal algal communities. British Phycological Journal, 18, 211.

Whittick, A., 1983. Spatial and temporal distributions of dominant epiphytes on the stipes of *Laminaria hyperborea* (Gunn.) Fosl. (Phaeophyta: Laminariales) in S.E. Scotland. *Journal of Experimental Marine Biology and Ecology*, **73**, 1-10.

Wiborg, F.K., 1946. Undersøkelser over oskellet (*Modiolus modiolus* (L.)). *Fiskeridirektoratets Skrifter* (ser. Havundsrsøkelser), **8**, 85. Wildish, D. & Peer, D., 1983. Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy. *Canadian*

Journal of Fisheries and Aquatic Sciences, **40** (S1), s309-s321.

Wildish, D.J. & Fader, G.B.J., 1998. Pelagic-benthic coupling in the Bay of Fundy. Hydrobiologia, 375/376, 369-380.

Wildish, D.J. & Kristmanson, D.D., 1985. Control of suspension feeding bivalve production by current speed. *Helgolander Meeresuntersuchungen*, **39**, 237-243.

Wildish, D.J., Fader, G.B.J., Lawton, P. & MacDonald, A.J., 1998. The acoustic detection and characteristics of sublittoral bivalve reefs in the Bay of Fundy. *Continental Shelf Research*, **18**, 105-113.

Wotton, D.M., O'Brien, C., Stuart, M.D. & Fergus, D.J., 2004. Eradication success down under: heat treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. *Marine Pollution Bulletin*, **49** (9), 844-849.