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Modiolus modiolus beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata

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

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***Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata.**
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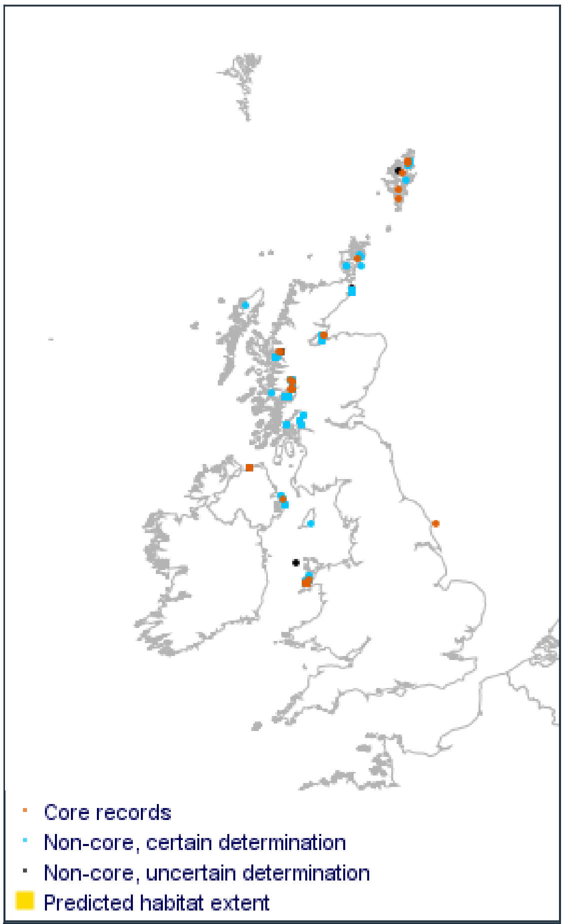

17-09-2018
Biotope distribution data provided by EMODnet Seabed Habitats (www.emodnet-seabedhabitats.eu)

Researched by Dr Heidi Tillin & Dr Harvey Tyler-Walters **Refereed by** This information is not refereed.

Summary

UK and Ireland classification

EUNIS 2008	A5.621	*Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata
JNCC 2015	SS.SBR.SMus.ModT	*Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata
JNCC 2004	SS.SBR.SMus.ModT	*Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata
1997 Biotope	CR.MCR.M.ModT	*Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata

Description

Modiolus beds on mixed substrata (cobbles, pebbles and coarse muddy sediments) in moderately strong currents or wave exposed areas, typically on the open coast but also in tide-swept channels of marine inlets. Ophiothrix fragilis are often common in this biotope along with the calcareous tubes of *Spirobranchus triqueter*, anemones such as *Alcyonium digitatum* and *Urticina felina* and hydroids such as *Abietinaria abietina* and *Sertularia argentea*. *Buccinum undatum* may also be important and in some areas the clam *Mimachlamys varia* may be frequent but not in the same abundances as in ModCvar. Little information on the infaunal component is given here although it is likely that it is very rich and may highlight more subtle differences in the *Modiolus* biotopes. This biotope is typified by examples off the north-west Lleyn Peninsula in N Wales and off Co. Down, Northern Ireland. (Information from Connor *et al*., 2004; JNCC, 2105).

Depth range

5-10 m, 10-20 m, 20-30 m, 30-50 m

Additional information

No text entered

Listed By

- none -

Further information sources

Search on:

G G JNCC

Habitat review

Ecology

Ecological and functional relationships

- *Modiolus modiolus* communities (clumps or beds) provide hard substratum in usually sedimentary areas. They accumulate a sediment of silt, organic rich faeces and pseudofaeces, and shell debris, forming raised beds, bound together by a matrix of byssus threads and horse mussels. Therefore, they significantly modify the habitat providing substratum, refuge and ecological niches for a wide variety of organisms.
- Horse mussel beds support a diverse assemblage of suspension feeders, including barnacles (e.g. *Balanus crenatus*) and tube worms (e.g. *Spirobranchus triqueter*), hydroids (e.g. *Sertularia argentea*), anthozoans such as *Alcyonium digitatum*, bryozoans such as *Alcyonidium mytili* and *Electra pilosa*, ascidians (e.g. *Dendrodoa grossularia*), and brittlestars such as *Ophiothrix fragilis* and *Ophiopholis aculata* (Comely, 1981; Connor *et al.*, 1997a; Holt *et al.*, 1998).
- Where present, red seaweeds and coralline algae are primary producers and are grazed by urchins, gastropods and chitons, however, fouling by algae and epifauna may be detrimental to the horse mussel bed (Witman, 1985; Holt *et al.*, 1998).
- Sea urchins, e.g. *Echinus esculentus* graze algae and epifauna on the horse mussel bed. Fouling organisms reduce the fitness of the horse mussels by reducing tissue weight and gametic development (Suchanek, 1985). Excessive fouling, especially by large algae such as kelp, increases drag and may result in removal of mussels by tidal streams, currents or wave action (see also *Mytilus edulis*) (Suchanek, 1985). Witman (1984; cited in Suchanek, 1985) noted that during 11 months of monitoring in the New England subtidal, 84% of fouled horse mussels were dislodged while 0% of un-fouled specimens were dislodged. Experimental removal of the sea urchin *Strongylocentrotus droebachiensis* from New England horse mussels beds, resulted in a 30 fold increase in dislodgement of horse mussels in the cleared areas due to the growth of kelps (Witman, 1984 cited in Suchanek, 1985; Holt *et al.*, 1998). Therefore, Suchanek (1985) suggested that a facultative mutualism (sea urchins are not exclusive to mussel beds) exists between the mussel beds and sea urchins, where horse mussels benefit from the grazing activity of sea urchins, while the sea urchins benefit from the refuge from predation provided by the bed.
- Witman (1985) demonstrated that the horse mussel beds in New England, USA provided a refuge from crab, lobster or fish predation for sea urchins, bivalves and brittlestars. He also showed that horse mussel beds provided a refuge from intense epifaunal grazing pressure by sea urchins. Horse mussel beds in British waters are also probably used as a refuge by similar species.
- Starfish, crabs, lobsters and fish are probably significant predators on horse mussel beds. Starfish, crabs, lobsters and fish are generalists taking epifauna and horse mussels as prey (Witman, 1985). Juvenile horse mussels are subject to intense predation pressure, probably from starfish (e.g. *Asterias rubens*), the whelk *Buccinum undatum*, and crabs (e.g. *Cancer pagurus*) until they reach over 45-60mm in shell length (Brown & Seed, 1977; Comely, 1981; Sebens, 1985). Intense predation pressure may account for the low levels of recruitment and the bimodal population structure seen in populations of *Modiolus modiolus*, i.e. a peak of large individuals and a variable peak of smaller horse mussels (Brown & Seed, 1977; Holt *et al.*, 1998). Witman (1985) noted that in New England horse mussel beds, crabs and lobsters were active at night while fish accounted for 71% of the

total prey taken during the day.
- The organic rich sediment that accumulates within and under the horse mussels bed supports an infauna of deposit feeders including polychaetes and holothurians (Comely, 1981; Witman, 1985; Brown & Seed, 1977; Holt *et al*., 1998).

Seasonal and longer term change

Holt *et al.* (1998) stated that dense horse mussel beds were thought to be very stable in the long-term, since they were observed in the same areas over long time periods. However, they noted that long-term changes in the *Modiolus modiolus* population structure, and their associated community had not been studied. Ojeda & Dearborn (1989) examined the community structure of rocky intertidal habitats in Maine, USA between August 1984 and October 1986, including *Modiolus modiolus* beds. They noted no significant change in community biomass or density during the study period. However, species number varied with season and was maximal in summer, intermediate in autumn and spring but minimal in winter. They suggested that seasonal changes were probably due to migration or changes in activity of some of the species. In addition, it is likely that some seasonal changes occur in the abundance or extent of algal species within this biotope. Holt *et al.* (1998) suggest that some variation in *Modiolus modiolus* population structure must occur given the variable and sporadic nature of recruitment in the species.

Habitat structure and complexity

Holt *et al.* (1998) suggested that most *Modiolus modiolus* communities consist of:

- very dense aggregations of horse mussel shells (living and dead) forming a single or multi-layered framework;
- a rich community of free-living and sessile epifauna and predators;
- a very rich and diverse community of species, with low abundance, which shelters between the shells and byssus threads of the horse mussels and thrives on the rich sediment, and
- an infauna living within the rich sediment deposits built up by the bed.

Examples include:

- epibionts such as barnacles (e.g. *Balanus crenatus* or *Balanus balanus*), tubeworms (e.g. *Spirobranchus triqueter*), and coralline algae living on shells of *Modiolus modiolus* (Comely, 1981; Holt *et al*., 1998)
- sessile epifauna include bryozoans, hydroids, anthozoans such as *Alcyonium digitatum*, serpulid worms, sponges, saddle oysters and red algae such as *Phycodrys rubens* (Holt *et al*., 1998);
- mobile epifauna include whelks, starfish, sea-urchins, top shells, nudibranchs, and many decapod crustaceans (Holt *et al*., 1998);
- the brittlestars *Ophiothrix fragilis* and *Ophiopholis aculata* are commonly found in crevices between the horse mussels (Comely, 1981; Holt *et al*., 1998);
- infauna may typically include the heart urchin *Spatangus purpureus*, and bivalves *Glycymeris* sp., *Astarte sulcata* and *Venus*, spp. (Holt *et al*., 1998) as well as polychaetes and holothurians (Witman, 1985). The 'deep Venus community' is particularly characteristic of the biotope CMX.ModMx (Connor *et al*., 1997a; Holt *et al*., 1998), and
- *demersal fish such as dragonets, small-spotted catshark (dogfish), butterfish, and sea scorpions (Holt et al., 1998).*

Productivity

Suspension feeding by the horse mussels and the suspension feeding community they support undoubtedly represent a significant contribution to secondary production in the benthic ecosystem (see Wildish & Fader, 1998). Filter feeding by horse mussel beds may be of great importance in channelling primary phytoplankton productivity to the benthos, termed 'benthic-pelagic' coupling. Navarro & Thompson (1997) demonstrated that *Modiolus modiolus* beds in Newfoundland fed on small phytoplankton but concentrated large diatoms in their pseudofaeces, and may contribute up to 40.9 mg dry weight per individual per day (faeces and pseudofaeces) hence cycling nutrients to the benthic ecosystem. Wildish & Fader (1998) reported that in the well mixed waters of the Bay of Fundy, horse mussel beds were able to feed on phytoplankton down to about 100m in depth and made a significant contribution to secondary benthic productivity (Holt *et al*., 1998; Wildish & Fader, 1998; Navarro & Thompson, 1997). In less well mixed areas, primary production reaches the benthos as organic particulates, detritus and dissolved organic matter. In shallow subtidal waters, or where light penetration is adequate for macroalgal growth, red algae contribute to primary productivity, and are probably utilized by a number of grazing species (see ecological relationships). However, no information on productivity levels were found.

Recruitment processes

- 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, 1978; Figure 3). 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).
- Established horse mussel beds are probably important for the recruitment (settlement and survival to maturity) of juveniles. Settlement within the byssus or mussel matrix of adults greatly increases the survival of juveniles in the face of intense predation pressure (Jones *et al*., 2000; Holt *et al*., 1998).
- Dense growth of foliose seaweeds or branching bryozoans and hydroids may provide an important settling area for bivalve spat, e.g. *Pecten maximus*, *Chlamys* spp. and *Aequipecten opercularis*, adults beds of which are often abundant in the vicinity of horse mussels beds (Holt *et al*., 1998).
- Recruitment in echinoderms is poorly understood, often sporadic and variable between locations and dependant on environmental conditions such as temperature, water quality and food availability. For example, in *Echinus esculentus*, planktonic development suggests considerable dispersal potential. However, recruitment is sporadic and Millport populations showed annual recruitment, whereas few recruits were found in Plymouth populations during Nichols studies between 1980-1981 (Nichols, 1984). Bishop & Earll (1984) suggested that the population of *Echinus esculentus* at St Abbs had a high density and recruited regularly whereas the Skomer population was sparse, ageing and had probably not successfully recruited larvae in the previous 6 years. In *Ophiothrix fragilis* recruitment success is heavily dependent on environmental conditions including temperature and food availability. In years after mild winters *Ophiothrix fragilis* occurred

in extremely high densities in the Oosterschelde estuary in Holland (Smaal, 1994). Populations seem to be stable in the long-term although there may be strong variation from year to year.
- Hydroids have limited dispersal potential due to a short planktonic larval stage, so that colonization is probably local. Recruitment would be dependent on currents and the proximity of hydroid communities.
- Bryozoa also have a short lived larva which does not travel far (see *Umbonula littoralis*). Similarly, the ascidian 'tadpole' larva has a very short planktonic life, dispersal is relatively poor and recruitment and colonization would depend on the proximity of nearby adult colonies in most species. Recruitment from distant colonies may take a long time.
- Red algae produce millions of non-motile spores, that may settle close to the adult or travel great distances depending on currents and turbulent deposition (Norton, 1992). For example, red algae colonized blocks within 26 weeks in the shallow subtidal (0.8m) and 33 weeks at 4.4m (Kain, 1975). *Delesseria sanguinea* was noted within 41 weeks (8 months) at 4.4m in one group of blocks and within 56-59 days after block clearance in another group of blocks. Recolonization occurred during winter months following spore release and settlement, but not in subsequent samples (Kain, 1975). This suggests that recolonization of *Delesseria sanguinea* in new areas is directly dependent on spore availability.

Time for community to reach maturity

Holt *et al*., (1998) point out that where impacts are severe enough to clear extensive areas of a horse mussel bed, recovery would be unlikely even in the medium term. They also noted that both the time required for small breaks in beds to close up due to growth of surrounding clumps, and the survival of clumps torn from the bed is not known. Witman (1984 cited in Suchanek, 1985) cleared 115cm^2 patches in a New England *Modiolus modiolus* bed. None of the patches were recolonized by the horse mussel after 2 years, 47% of the area being colonized by laminarian kelps instead (Witman pers. comm. cited in Suchanek, 1985). No details on longer term studies were found.
The horse mussel is long-lived and reproduction over an extended lifespan may compensate for poor annual recruitment. However, any factor that reduces recruitment is likely to adversely affect the population in the long-term. Any chronic environmental impact may not be detected for some time in a population of such a long -lived species.
Overall, therefore, while some populations are probably self-sustaining it is likely that a population that is reduced in extent or abundance will take many years to recover, and any population destroyed by an impact will require a very long time to re-establish and recover, especially since newly settled larvae and juveniles require the protection of adults to avoid intense predation pressure.

Additional information

No text entered

Preferences & Distribution

Habitat preferences

Depth Range	5-10 m, 10-20 m, 20-30 m, 30-50 m
Water clarity preferences	Field Unresearched

Limiting Nutrients	Field unresearched
Salinity preferences	Full (30-40 psu)
Physiographic preferences	Open coast
Biological zone preferences	Circalittoral, Lower infralittoral
Substratum/habitat preferences	Cobbles, Mixed, Pebbles
Tidal strength preferences	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Strong 3 to 6 knots (1.5-3 m/sec.)
Wave exposure preferences	Moderately exposed, Sheltered, Very sheltered
Other preferences	None found

Additional Information

Modiolus modiolus is a boreal species reaching its southern limit in British waters and it may be susceptible to long-term increases in summer water temperatures (Holt *et al.*, 1998). Little 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 & Kjrsvik, 1982). Extensive beds are most common on northern or western coasts but absent south of the Severn and Humber estuaries *Modiolus modiolus* beds are found in a variety of turbid and clear water environments (Holt *et al.*, 1998).

Species composition

Species found especially in this biotope

- *Modiolus modiolus*

Rare or scarce species associated with this biotope

-

Additional information

Modiolus modiolus beds support species rich, diverse communities (Holt *et al.*, 1998) which represent most of the major invertebrate groups (Brown & Seed, 1977). However estimates of species richness and descriptions of the communities vary, and depend on the sampling techniques used. Descriptions of the infauna are likely to be underestimates. Species numbers vary with season (Ojeda & Dearborn, 1989) and sampling time, e.g. predatory crabs are prevalent at night and fish more prevalent during the day (Witman, 1985).
The MNCR recorded 379 species within the MCR.ModT biotope. The following numbers of species were found within horse mussel communities, although not necessarily the biotope in question:

- 90 invertebrate taxa in horse mussel beds in Strangford Lough (Brown & Seed, 1977);
- 270 invertebrate taxa in horse mussel reefs on the north east of the Isle of Man (Holt & Shalla, unpublished; cited in Holt *et al.*, 1998);
- 89 invertebrate taxa in Scottish horse mussel beds (Comely, 1981);
- the horse mussel communities in St. George's Channel were described by Mackie *et al.* (1995), and

- the horse mussel communities of Northern Ireland, including MCR.ModT were described by Erwin *et al.* (1990).

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

Horse mussels (*Modiolus modiolus*) may occur as isolated individuals nesting in the sediment, scattered clumps or aggregations, with densities reaching up to 400 individuals/m^2 (Lindenbaum *et al*. 2008) and stretching patchily for between several square metres to kilometres on the subtidal shelf (Dinesen & Morton, 2014, and references therein). OSPAR (2009) indicated that patches that extended over >10 m^2 with >30% cover by mussels should definitely be classified as "bed". However, mosaics also occur where frequent smaller clumps of mussels influence ecosystem functioning so that for conservation and management purposes, lower thresholds can be accepted for defining beds (Rees, 2009).

Studies have identified between 100 and 200 macrofaunal taxa associated with *Modiolus modiolus*, while overall species numbers may reach ≥ 400 (Göransson & Karlsson, 1998; Rees *et al*. 2008; Göransson *et al*. 2010) at sites with soft substrata. Few of these species are endemic to *Modiolus* beds and have a facultative rather than obligate relationship with *Modiolus* beds. The sensitivity assessments, therefore, focus on *Modiolus modiolus* as the main characterizing species and bioengineer of the habitat. Grazing species may be important in controlling algal growth which can increase drag by water currents on the bed and result in individuals being swept away.

Resilience and recovery rates of habitat

Witman (1984, cited in Suchanek 1985) cleared 115 cm^2 patches in a New England *Modiolus modiolus* bed. None of the patches were recolonized by the horse mussel after 2 years, 47% of the area being colonized by laminarian kelps instead (Witman pers. comm., cited in Suchanek 1985). On Georges Bank in the Northwestern Atlantic, *Modiolus modiolus* larvae recruited onto test panels within two years (Collie *et al*. 2009), although due to slow growth (and recruitment) of the species it would take 10–15 years for clusters of large individuals to form. Similarly, Mair *et al.* (2000) reported recruitment into disturbed sediments a few years after a pipeline was laid (cited from OSPAR, 2009). Anwar *et al.* (1990) reported a substantial population on the legs of an oil rig, 10 years after installation, and suggested that growth was enhanced in this situation due to a lack of predation (OSPAR, 2009). The results suggest that in areas that are artificially cleared or free of predators, recruitment may be relatively rapid where there is a supply of larvae. However, the results refer to a dense settlement of juveniles rather than the development of reefs and such settlements may be relatively ephemeral or in habitats that are not suitable for the long-term establishment of a bed.

Modiolus modiolus is relatively long-lived. Individuals of 10 cm shell length from Northern Ireland were estimated to be between 14 and 29 years old (Seed & Brown 1975, 1978), and individuals from Shetland of 10 cm shell length were estimated to be between 11 and 17 years old (Comely, 1981). Anwar *et al.* (1990) report that the oldest individual studied, from the northern North Sea at a depth of 73–77 m, was approx. 48 years old. In Norway, *Modiolus modiolus* has been reported to become sexually mature at 3 years of age, although most individuals do so at an age of 5–6 (and up to 8) years (Wiborg 1946). Around the Isle of Man, the youngest mature individuals were 3–4 years old (Jasim & Brand 1989). In Canada, the earliest mature individuals were 4 years old, and most individuals did not reach maturity until the age of 7–8 years (Rowell 1967). In Northern Ireland, most individuals mature at a shell length of 4–5 cm (4–6 years), but some were already mature at a shell length of 1–2 cm (Seed & Brown 1977).

Reproduction and spawning duration vary between depth and location. Dinesen & Morton (2014) compared gametogenesis and spawning season in four subtidal populations of *Modiolus modiolus* from a depth of 15 m and showed that both may occur simultaneously. In Strangford Lough, gametogenesis and spawning may occur throughout the year, with peak months varying between years (Brown, 1984). Geographic differences play an important role in the timing of maturity and there appear to be differences between populations even within short distances at similar depths. Similarly, populations in the same area but at different depths show variation (Dinesen & Morton, 2014).

The larvae require approx. 4 weeks from fertilization to competency (Dinesen & Morton, 2014). Comely (1978) observed that spat settled on established adults, and larger individuals were found within the byssus thread where they had either settled or migrated to after shell settlement. Dinesen & Ockelmann (unpublished data, cited in Dinesen & Morton, 2014) observed that competent larvae settle preferentially in response to the exhalant water of adults. 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, also indicated that settlement of *Modiolus modiolus* larvae was directly enhanced by the presence of adults on the sea floor (Davoult *et al*. 1990). Where beds are cleared or reduced in size, recolonization may, therefore, be hampered by the lack of adults.

Recruitment is sporadic and highly variable seasonally, annually or with location (geographic and depth) and influenced by prevailing hydrographic conditions and current dynamics (Holt *et al*., 1998). For example settlement in Bristol Channel populations is dense but subsequent recruitment is low (Holt *et al*., 1998); regular recruitment occurs in populations in Strangford Lough and in two areas south east of the Isle of Man (Seed & Brown, 1978; Jasim & Brand, 1986); but very irregular recruitment, with gaps of many years, was reported for Norwegian (Wiborg, 1946) and Canadian populations (Rowell, 1967).
Scottish populations varied, with 'normal' recruitment occurring in areas of strong currents, resulting in a relatively young population, while recruitment was negligible in areas of quiet water resulting in an ageing population, and in a deep water population no recruitment had occurred for a number of years and the population was old, possibly senile and dying out (Comely, 1978).

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. The Strangford Lough populations appear to be self-recruiting (Brown 1990; Elsässer *et al*. 2013). 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 (Comely, 1978; Holt *et al*. 1998). Gormley *et al*., (2015) developed biophysical models for larval dispersal in the Irish Sea validated by DNA studies indicate that populations of *Modiolus modiolus* in the North Irish Sea are connected. Genetic analysis was consistent with those of the biophysical models and indicated moderately significant differentiation between the Northern Ireland populations and those in the Isle of Man and Wales. Simulations of larval dispersal over a 30 day pelagic larval duration (PLD) suggest that connectivity over a spatial scale of 150km is possible between some source and sink populations. However, it appears unlikely that larvae from Northern Ireland will connect directly with sites on the Llŷn or Isle of Man. It also appears unlikely that larvae from the Llŷn connect directly to any of the other sites (Gormley *et al*., 2015).

Habitat restoration projects may translocate stock to repopulate areas of suitable habitat (Elsässer *et al*., 2013). No evidence was found for detrimental, genetic effects arising from this practice, although there is potential also for the movement of pathogens and non-indigenous, invasive species. In Strangford Lough, restoration efforts translocated *Modiolus modiolus* clumps within the Lough as it was considered that individuals from outside populations would be less suitable (Fariñas-Franco *et al*., 2013, 2016). Translocation of individuals was demonstrated to support larval settlement on artificial reefs, when measured against cultch alone and is a useful technique to support habitat restoration (Fariñas-Franco et al., 2016). Inter-site differences in shell morphology, reflecting phenotypic differences have been observed between populations that relate to adaptation to local environmental conditions . Translocating individuals with ecophenotypes that are different to local populations may impact on the success of translocation may result in negative impacts on local populations through gene flow.

Resilience assessment. Recruitment in *Modiolus modiolus* is sporadic and highly variable seasonally, annually or with location (Holt *et al*., 1998). Dinesen & Morton (2014) state that, post impact recovery times are long and dependent on local and mega-population distributions. Any factor that reduces recruitment is likely to adversely affect the population in the long-term. However, any chronic environmental impact may not be detected for some time in a population of a relatively long-lived species and populations may survive as ‘relicts’ in habitats that are now unsuitable (OSPAR, 2009). Overall, therefore, while some populations are probably self-sustaining it is likely that a population that is reduced in extent or abundance will take many years to recover to a mature bed, and any population destroyed by an impact will require a very long time to re-establish and recover, especially since larvae depend on adults for settlement cues and juveniles require the protection of adults to avoid intense predation pressure.

The available evidence for *Modiolus modiolus* suggests that recovery from significant impacts could be inhibited by the lack of adults to provide settlement cues and protection to larvae and juveniles. Therefore, where resistance is assessed as ‘None’, resilience is assessed as ‘Very Low’ (>25 years). Resilience is assessed as ‘Low’ (10 to 25 years) where resistance is assessed as ‘Low’ (removal of 25-75% of individuals). Resilience is assessed as ‘Medium’ (2-10 years) where less than 25% of the bed is removed ('Medium' resistance) and the habitat remains suitable for recolonization. It should be noted that these recovery rates pertain to beds of *Modiolus modiolus*, not biotopes where sparse individuals occur.

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

Hydrological Pressures

	Resistance	Resilience	Sensitivity

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

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). Observations on *Modiolus modiolus* exposed to high temperatures suggest that this species is restricted by upper limiting sea water temperatures of 23°C (Read & Cummings 1967). Although individuals may survive short-term exposure to higher temperatures as Read (1967) found that in intertidal pools most *Modiolus modiolus* survived (for at least a week) following exposure of temperatures that rose from 19° to 32.5°C over 5.5 hours.

Subtidal populations are protected from major, short-term changes in temperature by their depth. However, Holt *et al*. (1998) suggested that because *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 the 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 (Strain *et al*., 2012).

Sensitivity assessment. *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 long-term increases in temperature. Adult populations may be unaffected at the pressure benchmark and, in such long-lived species, an unfavourable recruitment may be compensated for in the following year. Resistance to an acute and chronic change in temperature at the pressure benchmark is therefore assessed as 'High' and recovery as 'High' (by default) and the biotope is considered 'Not Sensitive'. It should be noted that the timing of acute changes may lead to greater impacts, temperature increases in the warmest months may exceed thermal tolerances whilst changes in colder periods may stress individuals acclimated to the lower temperatures. Sensitivity (particularly of southernmost populations) to longer-term, broad-scale perturbations such as increased temperatures from climate change would, however, be likely to be greater, based on the extent of the impact.

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

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 and Kjørsvik (1982) suggested that its inability to tolerate temperature change was a factor preventing the horse mussel from colonising 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.

Observations on a shallow (10m depth), *Modiolus modiolus* population from the Gulf of Maine, found that individuals undergo seasonal thermal compensation, altering enzyme concentrations to maintain growth and reproduction as temperatures decrease (Lesser & Kruse, 2004). The study does not, however, indicate responses to rapid temperature decreases at the pressure benchmark and mussels were kept at temperatures they would typically experience, rather than temperatures outside the usual annual range.

Sensitivity assessment. *Modiolus modiolus* is a boreal species, with beds in higher latitudes exposed to colder temperatures than experienced at the southern limit of its range in the UK. Beds of *Modiolus modiolus* are therefore considered to have 'High' resistance to decreased temperatures at the benchmark. Resilience is assessed as 'High' (by default) and this biotope is considered to be 'Not sensitive'.

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

Modiolus modiolus is an osmoconformer. 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 *M. modiolus* to increased salinities is provided by Pierce (1970). *Modiolus modiolus* was exposed to a range of salinities between 1.5 and 54 psu, at 27 to 41 psu *Modiolus modiolus* survived for 21 days (the duration of the experiment) (Pierce, 1970).

Sensitivity assessment. The only evidence to support this assessment is provided by short-term experiments. As this biotope has only been recorded from areas of full salinity (Connor *et al*., 2004) a change at the pressure benchmark refers to an increase to hypersalinity (>40 ppt). No direct evidence was available to support this assessment but over the course of a year, an increase in salinity may lead to mortality of *Modiolus modiolus*. Biotope resistance is, therefore, assessed as 'Low' and resilience as 'Low' so that sensitivity is assessed as 'High'.

Salinity decrease (local)	Low Q: High A: Medium C: Medium	Low Q: High A: Low C: High	High Q: High A: Low C: Medium

Local populations may be acclimated to the prevailing salinity regime and may, therefore, exhibit different tolerances to other populations subject to different salinity conditions and therefore caution should be used when inferring tolerances from laboratory experiments and from populations in different regions. The sensitivity of *Modiolus modiolus* to changes in salinity at the benchmark can be inferred from distribution information and from laboratory experiments that have exposed individuals to decreased salinities.

Some populations of *Modiolus modiolus* are present in areas where salinities are lower than typical, fully marine conditions. From the Baltic Sea distribution pattern, Dinesen & Morton, (2014 and references therein) inferred that the lower, long-term salinity tolerance of adult *Modiolus modiolus* is likely to be approx. 26 units. This is supported by observations of Davenport & Kjørsvik (1982) who 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 subtidally 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. The biotope records suggest that this biotope only occurs in the UK in full salinity (30-40 ppt) habitats (Connor *et al*., 2004).

Laboratory experiments exposing *Modiolus modiolus* to reduced salinity water have demonstrated short-term effects. Pierce (1970) exposed *Modiolus* spp. to 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. The available evidence indicates that *Modiolus modiolus* are osmoconformers able to tolerate decreases in salinity for a short period. However, a decrease in salinity at the pressure benchmark (a decrease in one MNCR unit) from full salinity to variable (18-40 ppt) would be considered to result in the mortality of all adults within the biotope over the course of a year. This assessment is supported by observed distribution across different salinity regimes (Connor *et al*., 2004, Dineson & Morton, 2014) and laboratory experiments (Shumway, 1977, Pierce, 1970) which suggest that a change at the pressure benchmark would exceed the lower threshold tolerance of adults over the course of a year). Therefore, a resistance of 'High' is suggested, with a resilience of 'Low' and resultant sensitivity of 'High'.

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

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 supply food in suspension, but that 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. This biotope occurs where tidal streams are strong (1.5-3 m/s) to moderately strong, from 0.5-1.5 m/s (JNCC, 2015).

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/m^2 have been recorded from the Faroese shelf (Dinesen, 1999) where maximal tidal current speed has been estimated to be between 0.79 and 0.98 m/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.

Comely (1978) suggested that areas exposed to strong currents required an increase in byssus production, at energetic cost, and resulted in lower growth rates. At water velocities exceeding 16 cm/s in a flume tank, Carrington *et al*., (2008) observed that *Modiolus modiolus* individuals could not extend the foot beyond the shell to form and attach byssus threads. However, the mussel bed reduces water flow rates by increasing drag through friction. Carrington *et al*., (2008) observed that mussel beds of *Mytilus trossulus* and *Mytilus galloprovincialis* in laboratory and field studies were able to reduce flow rates between 0.1 and 10% of free-stream velocity. This modification of flow may enhance suspension feeding in areas of high current flow and allow byssus production to continue (Carrington *et al*., 2008).

Wildish *et al*., (2000) examined suspension feeding in *Modiolus modiolus* in a flume tank and noted that individuals kept the exhalant and inhalant siphons open over the range of flow rates studied, from 0.12-0.63 m/s. However, the inhalant siphon closed by about 20% in currents above 0.5m/s. Although partial closure of the inhalant siphon may reduce food intake this may be compensated by the greater abundance of food supply in higher currents. Widdows *et al*., (2002) found that there was also a slight decline in feeding rate of *Mytilus edulis* at current velocities below 0.05 m s/s, which was probably due to algal cell depletion and greater recirculation of near bed water by the group of mussels.

Fouling by epifauna and algae in the infralittoral may also decrease the population's resistance to increased water flow. Witman (1984, cited in Suchanek, 1985) found that over 11 months in New England, 84% of fouled mussels were dislodged in comparison with 0% of unfouled individuals. Conversely, attached epifauna may reduce turbulence and flow, which could be beneficial.

Changes in water flow may also be a spawning cue, although the available evidence does not strongly support this hypothesis. Schweinitz & Lutz, (1976) observed spontaneous, spawning in a group of *Modiolus modiolus* individuals kept in a tank when the water flow stopped while previous attempts to induce spawning by various methods had failed. However, subsequent attempts to induce spawning by stopping the water flow failed (De Schweinitz & Lutz, 1976). A similar spawning response in *Mytilus edulis* to the cessation of flow (Williamson, 1997) was cited (De Schweinitz & Lutz, 1976).

The density of *Modiolus modiolus* and the character of the substratum will influence the level of sediment erosion following increases in water flow rates. Widdows et al (2002) conducted a series of experiments in a flume on sediment erodibility in relation to the density of *Mytilus edulis* and substratum type. In sand sediments, sediment erosion was greater where mussel coverage was between 25% and 50% due to scouring around clumps. Bare sediments (no mussels) and sediments with full coverage had lower rates of erosion.

Sensitivity assessment. Flow rates are an important factor for *Modiolus modiolus* and influence food transport, feeding rate and sediment erosion and transport which may reduce feeding success where high rates of inorganic particles are present in the water column. *Modiolus modiolus* may be sensitive to both increases and decreases in flow. Direct evidence is not available to identify the optimal range and increases may be moderated by the bed structure and density which will depend on the degree of recession into sediments and the size and type of associated epifauna (if any). Adult *Modiolus modiolus* may have 'High' resistance to changes in water flow rates at the pressure benchmark based on the occurrence of this biotope in strong or moderately strong tidal streams. Changes in flow rates that alter feeding success through changes in clearance rates and food supply and larval recruitment, however, may lead to the presence of beds, composed of ageing adults, that are not sustainable in the long-term. As this biotope occurs in a wide range of flow speeds, resistance is assessed as 'High', resilience as 'High' (by default0 and the biotope is assessed as 'Not sensitive'. changes outside the pressure benchmark could lead to an increase in species richness and reclassification to another *Modiolus modiolus* biotope.

Emergence regime changes	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR
Wave exposure changes (local)	High Q: High A: Medium C: Medium	High Q: High A: High C: High	Not sensitive Q: High A: Medium C: Medium

The majority of *Modiolus modiolus* populations are subtidal and unlikely to be affected by wave action directly. However, increased wave action results in increased water flow in the shallow subtidal. Wave mediated water flow tends to be oscillatory, i.e. move back and forth (Hiscock, 1983), and may result in dislodgement or removal of individuals. The mussels, *Mytilus edulis*, *Perna perna* and *Mytilus galloprovincialis* have been shown to increase byssus production in response to agitation and wave action (Young, 1985, Zardi *et al.*, 2007) and *Modiolus modiolus* may respond similarly. The intolerance of semi-infaunal or infaunal populations probably owes more to the nature of the substratum rather than their attachment. Populations on mobile sediment may be removed by strong wave action due to removal or changes in the substratum. No information concerning storm damage was found. Shallow, nearshore subtidal populations in Strangford Lough were exposed to wave mediated flows of 0.1 m/s (Elsäßer et al. 2013).   Decreased wave action may allow horse mussel beds to extend into shallower depths, however, the rates of increase in bed size are likely to be slow, probably much longer than the benchmark level.

Sensitivity assessment. No direct evidence was found to assess sensitivity to changes at the pressure benchmark. This biotope is recorded from moderately wave exposed to very wave sheltered conditions in tide-swept conditions so that water flow is probably a more important structuring factor than wave exposure, so that a 3-5% change in significant wave height (the benchmark level) is unlikely to be significant. Therefore, lower infralittoral and circalittoral beds in mixed sediment were considered to have ‘High’ resistance and ‘High’ resilience at the pressure benchmark to increases and decreases in wave height and are therefore assessed as ‘Not Sensitive’ at the benchmark level.

Chemical Pressures

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

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

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

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

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

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

Radionuclide contamination	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence

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

This pressure is **Not assessed**.

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

Theede *et al.* (1969) examined the relative tolerance of gill tissue from several species of bivalve to exposure to 0.21 mg/l O2 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*.

Sensitivity assessment. While it is difficult to extrapolate from tissue resistance to whole animal resistance (taking into account behavioural adaptations such as valve closure) the evidence suggests that horse mussels are more, or at least similarly, tolerant of hypoxia and hydrogen sulphide than the common mussel. In addition, most bivalve molluscs exhibit anaerobic metabolism to some degree. Therefore, a resistance of 'High' has been recorded at the benchmark level and resilience is assessed as 'High' (based on no effect to recover from). *Modiolus* beds are therefore considered to be 'Not sensitive' at the pressure benchmark. Resistance is likely to be influenced by temperature. An oxygen debt may induce wide valve gape and potentially increase susceptibility to predation. Wide valve gape is noted in Hutchison *et al*., (2016) as a response after unburial and is suggested to be due to an oxygen debt.

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

Navarro & Thompson (1996) suggested that *Modiolus modiolus* was adapted to an intermittent and often inadequate food supply. The persistence of a horse mussel population in the vicinity of a sewage sludge dumping site (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. However, eutrophication may have indirect adverse effects, such as increased turbidity, increased risk of deoxygenation (see above) and the risk of algal blooms. 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 outbreaks of paralytic shellfish poisoning in which bivalves accumulate toxins from algal blooms, although a direct causal effect required further research.

However, while algal blooms may have sub-lethal effects, the biotope is 'Not sensitive' at the benchmark level, which assumes compliance with environmental standards.

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

Little direct evidence was available to support the assessment of this pressure, which is largely based on expert judgement. In areas of strong tidal flow where some *Modiolus modiolus* beds are found, deposits of organic matter may be removed fairly rapidly mitigating the impact, although some deposits will be trapped within crevices and spaces where they may be utilised by the infaunal deposit feeding community. Where currents are weaker, as in some of the sheltered lochs and similar areas where beds occur, organic deposits may be removed more slowly and impacts may be greater. The persistence of a horse mussel population in the vicinity of a sewage sludge dumping site (Richardson *et al*., 2001) suggests that the species is tolerant of high levels of organic matter. Beds of *Modiolus modiolus* enrich the surrounding sediment via faeces and pseudofaeces so that the bed accumulates deposits rich in organic matter and increases in height compared to the surrounding seabed. 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. At the pressure benchmark, which refers to enrichment rather than gross organic pollution, *Modiolus modiolus* is considered to have 'High' resistance and hence, 'High' resilience. This biotope group is therefore considered to be 'Not Sensitive'.

Physical Pressures

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

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

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

The introduction of artificial hard substratum is considered at the pressure benchmark level and it is noted that *Modiolus modiolus* can colonise bedrock and artificial structures. On Georges Bank in the Northwestern Atlantic, *Modiolus modiolus* larvae recruited onto test panels within two years

(Collie *et al*. 2009). Anwar *et al*. (1990) reported a substantial population on the legs of an oil rig, 10 years after installation. It was suggested that growth was enhanced in this situation due to a lack of predation (OSPAR, 2009). The results suggest that on suitable surfaces, recruitment may be relatively rapid where there is a supply of larvae. However, the results refer to a dense settlement of juveniles rather than the development of reefs and the examples cited were habitats that were not suitable for the long-term establishment of a natural bed. *Modiolus modiolus* is also found on natural bedrock but again, a hard substrate is not suitable for the establishment of a natural bed, equivalent to the biotope desciption.

Sensitivity assessment. The resistance of the biotope to a change to artifical or natural hard is assessed as 'None' (loss of >75% of extent) as these surfaces are not suitable for natural beds. Resilience (following habitat recovery) is assessed as 'Very Low' (at least 25 years, or negligible recovery). Sensitivity, based on combined resistance and resilience is assessed as 'High'.

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

The change in one Folk class is considered to relate to a change in classification to adjacent categories in the modified Folk triangle (Long, 2006). For the mixed sediments that characterize this biotope the sediment changes considered may be to coarser or finer sediments. *Modiolus modiolus* is found on and in a variety of substrata ranging from fine mud with shells and gravel to bedrock. Comely (1978) found *Modiolus modiolus* in different types of sediment at varying densities, with low densities (mean 4 individuals/m^2) in clean gravel, stones and small boulders and at higher densities (mean 10 individuals/m^2 in fine muddy sand and silty sand with coarse gravel overlain by clean coarse sand with boulders). Differences in shell morphology between habitat types, has been observed in response to currents, sediment type and density (Fariñas-Franco *et al*., 2016). Changes in habitat may, therefore, result in individuals being less suited to the changed conditions. With potential effects on fitness, condition and survivability.

Based on ROV and SCUBA survey in Strangford Lough, Elsässer *et al*. (2013) modelled suitable habitat and found that substratum type was a key predictor of distribution of beds. The occurrence of the remaining beds was strongly linked to the presence of finer substrata, such as sand and mud, and negatively correlated with coarser substratum types such as bedrock, boulders and cobbles. These findings indicate that changes in seabed type are likely to alter habitat suitability for beds (and lead to biotope reclassification where the biotope description is substrate specific).

Sensitivity assessment. Given the wide range of substratum types occupied by this species, a change in sediment type is not considered to negatively impact habitat suitability at the level of the individual, however, as older horse mussels may be adapted, through shell morphology, to specific habitats and changes in sediment type may alter fitness and survivorship. However, the biotope group refers specifically to beds of *Modiolus modiolus* occurring in mixed sediments, rather than individuals. Based on the available evidence a change to coarse sediments may be more detrimental to the biotope than a change to finer sediments. As the biotope classification refers specifically to mixed sediments, an increase in fine or coarse sediments to the degree that sediments are re-classified would severely reduce habitat suitability. Resistance is therefore assessed as 'None' (loss of >75% of extent), resilience (following habitat recovery) is assessed as 'Very Low' (10 -25 years, or negligible recovery), as a change at the pressure benchmark is permanent.

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

Modiolus modiolus is found on and in a variety of substrata ranging from fine mud with shells and gravel to bedrock. The process of extraction is considered to remove sediment to 30cm depth and the horse mussel bed and associated biota, as beds of *Modiolus modiolus* are sessile and occur either on or within the sediment. No direct evidence for resistance and recovery to this pressure was found and the sensitivity assessment is therefore based on expert judgement and species traits.

Sensitivity assessment. The process of extraction is considered to remove all members of the biotope group as *Modiolus modiolus* are sessile. Resistance is therefore assessed as ‘None’, based on expert judgment but supported by the literature relating to the position of these species, on or within the seabed. At the pressure benchmark, the exposed sediments are considered to be suitable for recolonization almost immediately following extraction. Recovery will be mediated by the scale of the disturbance and the suitability of the sedimentary habitat. Local migration of adults could re-populate very small defaunated patches and passive transport of adults via water movements may occur around the disturbed edges of beds. Where larger areas have been affected by extraction, recovery is most likely to occur via larval recolonisation but the removal of adults is likely to reduce the chances of successful settlement (see recovery section). Resilience is considered to be ‘Very low', for the bed of *Modiolus modiolus* (25 or more years or negligible recovery). Sensitivity based on resistance and resilience is therefore categorised as ‘High’.

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

As *Modiolus modiolus* are large, sessile and present on sediment surfaces or shallowly buried, individuals will be exposed to abrasion of the surface of the seabed. Abrasion from towed fishing gear (e.g. scallop dredges) is known to flatten clumps and aggregations and may break off sections of raised reefs and probably damages individual mussels (Holt *et al*., 1998), as described below in the ‘penetration and or disturbance’ pressure’ which assesses the impacts of both abrasion and sub-surface damage. Older individuals can be very brittle due to infestations of the boring sponge *Cliona celata* (Comely 1978). Abrasion will also damage or remove associated biota.
Sensitivity assessment. Abrasion at the surface only is considered likely to flatten clumps and dislodge and break individuals. Resistance is assessed as ‘Low’ (damage or loss to 25-75% of the population), although the significance of the impact for the bed will depend on the spatial scale of the pressure footprint. Resilience is assessed as ‘Low’ (10-25 years), and sensitivity is assessed as ‘High’. Epifauna associated with the bed is also likely to be damaged and removed.

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

As *Modiolus modiolus* are large, sessile and shallowly buried, individuals are unable to escape from penetration and disturbance of the substratum and clear evidence exists for declines in the extent and density of beds exposed to activities that lead to this pressure. The associated attached epifauna and infauna are also likely to be damaged and removed by this pressure.

Evidence for long-term declines in response to abrasion and sub-surface penetration pressures, resulting from mobile gears has been found from surveys and monitoring in areas where beds have been impacted. Horse mussel beds in Strangford Lough in Northern Ireland have suffered notable declines in extent. Magorrian & Service (1998) reported that queen scallop trawling resulted in flattening of horse mussel beds and disruption of clumps of horse mussels and removal of emergent epifauna in Strangford Lough. They suggested that the emergent epifauna were more intolerant than the horse mussels themselves but were able to identify different levels of impact, from impacted but largely intact to few *Modiolus modiolus* intact with lots of shell debris (Service & Magorrian 1997; Magorrian & Service 1998).

Comparisons of dive survey data sets collected in Strangford Lough in 1975-1983 and 2005-2007, demonstrated further declines in *Modiolus modiolus*, the bivalves *Aequipecten irregularis* and *Chlamys varia* and some erect sessile fauna between the survey periods (Strain *et al*., 2012). Strain *et al*. (2012) concluded that the epifaunal assemblage in Strangford Lough had shifted due to the period of intensive fishing for the queen scallop (*Aequipecten irregularis*) between 1985 and 1995. Strain *et al*. (2012) noted that although all mobile fishing gear was banned in 2004, there were no detectable differences that indicate recovery of epifaunal communities, including *Modiolus modiolus* beds between 2003 and 2007 surveys, seven years after the period of intensive fishing for queen scallops.

Cook *et al*. (2013) were able to examine the effects of a single pass by a scallop dredge on *Modiolus modiolus* beds off the Lleyn Peninsula and an otter trawl on the northeast of the Isle of Man. The tracks from the mobile gears were observed during routine bed monitoring and the observations are based on normal fishing activities rather than designed experiments. The trawl resulted in a 90% reduction in the number of epifauna while the scallop dredge resulted in a 59% reduction. At both sites mean *Modiolus modiolus* abundance declined, with visible flattening of clumps in response to dredging. No evidence of recovery was recorded at the Isle of Man site a year after impact was first recorded. Mean abundance of *Modiolus modiolus* within quadrats was 63.8 (SD 20.7) within the unimpacted area and 40.7 (SD 15.4) within the scallop dredge impact at the Lleyn peninsula.

Kenchington *et al*. (2006) examined the effects of multiple passes of an otter trawl on benthic communities on the Western Bank on Canada's Scotian shelf in the northwest Atlantic. The community was dominated (76%) by *Modiolus modiolus* attached to rocks, embedded in the seabed or in small groups but was not considered to represent a *Modiolus* reef habitat. The transect was trawled 12-14 times, on three occasions over a 20 month period. As a result, the epifauna was reduced (from 90% to 77% contribution to the community). The most marked decline was in *Modiolus modiolus* abundance, which declined by approximately 80% to 60% of the community, (a reduction in biomass from approximately 2753 g before trawling in 1997 to 987 g after trawling in 1999) due to direct damage from the trawl and subsequent consumption by predators and scavengers.

Sensitivity assessment. Based on the available evidence, resistance to a single instance of penetration and disturbance at the pressure benchmark is assessed as 'Low' (loss of 25-75%), and resilience is assessed as 'Low' (> 25 years). Sensitivity is, therefore assessed as 'High'. Due to the low levels of recovery, repeated impacts are likely to result in the loss of reefs.

Changes in suspended solids (water clarity)	High Q: Medium A: Low C: NR	High Q: High A: High C: High	Not sensitive Q: Medium A: Low C: Low

Changes in light penetration or attenuation associated with this pressure are not relevant to *Modiolus modiolus biotopes*, 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 beds*. Horse mussels are selective feeders and can reject inorganic particles or larger, less nutrient rich phytoplankton in the form of pseudofaeces (Navarro & Thompson, 1997). *Modiolus modiolus* is found in a variety of turbid and clear water conditions (Holt *et* *al*., 1998). Muschenheim & Milligan (1998) noted that the height of the horse mussel beds in the Bay of Fundy positioned them within the region of high quality seston while avoiding high levels of re-suspended inorganic particulates (2.5-1500 mg/l) at the benthic boundary layer. An increase in suspended inorganic solids may reduce feeding efficiency and where the concentration exceeds tolerances, individuals may close valves and cease feeding.

Decreases in turbidity may increase phytoplankton productivity and potentially increase food availability. Therefore, horse mussel beds may benefit from reduced turbidity.

Sensitivity assessment. No directly relevant empirical evidence was found to assess this pressure. Resistance to this pressure is assessed as 'High' as an increase in turbidity may impact feeding and growth rates but not result in mortality of adults. Resilience is assessed as 'High' (by default) and the biotope is assessed as 'Not Sensitive' to changes in turbidity at the benchmark level.

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

Modiolus modiolus are unable to actively emerge from sediments if buried. In areas of strong tidal flow where some *Modiolus modiolus* beds are found, deposits of silt may be removed fairly rapidly, although some silts will be trapped within crevices and spaces. Mass Accumulation Rates of 0.63±0.09 g cm^{2} year-1) following bottom trawling in Strangford Lough were suggested to act as a driver for potential negative effects on the physiological condition of remnant populations of *Modiolus modiolus* by Strong & Service (2008). In a series of burial experiments, Hutchison *et al*. (2016) tested the response of individuals to burial under three depths of sediment (2, 5 and 7cm), three sediment fractions (coarse-1-2mm; medium-fine-0.25-0.95 mm and fine-0.1-0.25 mm) and five burial durations (2,4,8,16,32 days). *Modiolus modiolus* could not re-emerge from sediments and mortality increased with duration of smothering and the proportion of fine particles in the smothering material, the depth of burial did not alter mortality rates. Buried individuals survived for 8 days without apparent mortality but by 16 days cumulative mortality was greater than 50% (Hutchison *et al*., 2016).

Sensitivity assessment. The experiments by Hutchison *et al*., (2016) show that duration of burial is a key factor determining survival, burial under even small amounts of fine sediment (2 cm) for prolonged durations may result in mortality. Site-specific hydrodynamics that influence the mobility of deposited sediments will mediate resistance. As this biotope occurs in tide-swept conditions a fine sediment deposit may be removed relatively rapidly, limiting mortality (although cohesiveness of deposit and footprint will influence the duration of the deposit, if large areas are affected sediments may be shifted rather than removed), resistance is assessed as 'Medium' as some mussels within the bed may be smothered for longer than a week and begin to die before the overburden is removed. Resilience is assessed as 'Medium' and sensitivity is therefore categorised as 'Medium'.

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

Modiolus modiolus are unable to actively emerge from sediments if buried. In areas of strong tidal flow deposits of silt may be removed fairly rapidly, although some silts will be trapped within crevices and spaces. Where currents are weaker, deposits may be removed more slowly and impacts may be greater. Mass Accumulation Rates of 0.63±0.09 g cm^{2} year-1) following bottom trawling in Strangford Lough were suggested to act as a driver for potential negative effects on the physiological condition of remnant populations of *Modiolus modiolus* by Strong & Service (2008). In a series of burial experiments, Hutchison *et al*. (2016) tested the response of individuals to burial under three depths of sediment (2, 5 and 7cm), three sediment fractions (coarse-1-2mm; medium-fine-0.25-0.95 mm and fine-0.1-0.25 mm) and five burial durations (2,4,8,16,32 days). *Modiolus modiolus* could not re-emerge from sediments and mortality increased with duration of smothering and the proportion of fine particles in the smothering material, the depth of burial (at 2-7 cm deposit thickness) did not alter mortality rates. Buried individuals survived for 8 days without apparent mortality but by 16 days cumulative mortality was greater than 50% (Hutchison *et al*., 2016).

Sensitivity assessment. The experiments by Hutchison *et al*., (2016) show that duration of burial is a key factor determining survival, burial under even small amounts of fine sediment (2 cm) for longer than 8 days could lead to significant mortality. Site-specific hydrodynamics that influence the mobility of deposited sediments will mediate resistance, as the deposit at the pressure benchmark is substantial (30 cm) it is likely that the deposit will persist for some time (particularly if it consists of cohesive, fine particles) before removal. As this biotope may occur in sheltered conditions, resistance is assessed as 'Low' as some mussels may be smothered for longer than a week and begin to die before the overburden is removed. Resilience is assessed as 'Low' and sensitivity is therefore categorised as 'High'. The assessment is based on responses to a much thinner deposit of sediment and survival may be influenced by other factors such as temperature.

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

Not assessed.

Electromagnetic changes	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence.

Underwater noise changes	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence was found to assess the sensitivity of *Modiolus modiolus* to this pressure. However, experiments have demonstrated that *Mytilus edulis* show sensitivity to substrate-borne vibration, and it is possible that beds of *Modiolus modiolus* will also be affected by underwater noise. Behavioural changes (valve closure), in *Mytilus edulis*, were observed in experiments in in response to vibration stimulus (Roberts *et al*., 2015). Thresholds were shown to be within the range of vibrations measured in the vicinity of anthropogenic operations such as pile driving and blasting. The responses show that vibration is likely to impact the overall fitness of both individuals and mussel beds of *Mytilus edulis* due to disruption of natural valve periodicity, which may have ecosystem and commercial implications (Roberts *et al*., 2015).

Introduction of light or shading	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence.

Barrier to species movement	Medium Q: Low A: NR C: NR	Medium Q: High A: Low C: High	Medium Q: Low A: Low C: Low

Modiolus modiolus recruitment is sporadic and highly variable seasonally, annually or with location (geographic and depth) and influenced by prevailing hydrographic conditions and current dynamics (Holt *et al*., 1998) (see 'Resilience and recovery rates' above). For example, Scottish populations varied, with 'normal' recruitment occurring in areas of strong currents, resulting in a relatively young population, while recruitment was negligible in areas of quiet water resulting in an ageing population, and in a deep water population no recruitment had occurred for a number of years and the population was old, possibly senile and dying out (Comely, 1978). Comely (1978) suggested that recruitment was dependent on larvae from outside the area in areas of free water movement but, 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. The Strangford Lough populations appear to be self-recruiting (Brown 1990; Elsässer *et al*. 2013). 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 dependent on recruitment from other areas, which is in turn dependent on the local hydrographic regime (Holt *et al*. 1998).

As the larvae of *Modiolus modiolus* are planktonic and are transported by water movements, barriers that reduce the degree of tidal excursion may alter the supply of *Modiolus modiolus* to suitable habitats from source populations. However, the presence of barriers may enhance local population supply by preventing the loss of larvae from enclosed habitats. This species is, therefore, potentially sensitive to barriers that restrict water movements, whether this will lead to beneficial or negative effects will depend on whether enclosed populations are sources of larvae or are ‘sink’ populations that depend on outside supply of larvae to sustain the local population.

Sensitivity assessment. As this habitat is potentially sensitive to changes in tidal excursion and exchange, resistance is assessed as ‘Medium’ and resilience as ‘Medium’. Therefore, sensitivity is assessed as ‘Low’. It should be noted that offshore circalittoral habitats are unlikely to be exposed to this pressure.

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

Not relevant’ to seabed habitats. NB. Collision by grounding vessels is addressed under ‘surface abrasion’.

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

Not relevant.

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

Habitat restoration projects may translocate stock to repopulate areas of suitable habitat (Elsässer *et al*., 2013). No evidence was found for detrimental, genetic effects arising from this practice, although there is potential also for the movement of pathogens and non-indigenous, invasive species. In Strangford Lough, restoration efforts translocated *Modiolus modiolus* clumps within the Lough as it was considered that individuals from outside populations would be less suitable (Fariñas-Franco *et al*., 2013, 2016). Translocation of individuals was demonstrated to support larval settlement on artificial reefs, when measured against cultch alone and is a useful technique to support habitat restoration (Fariñas-Franco et al., 2016).

Gormley *et al*., (2015) developed biophysical models for larval dispersal in the Irish Sea validated by DNA studies indicate that populations of *Modiolus modiolus* in the North Irish Sea are connected. Genetic analysis was consistent with those of the biophysical models and indicated moderately significant differentiation between the Northern Ireland populations and those in the Isle of Man and Wales. Simulations of larval dispersal over a 30 day pelagic larval duration (PLD) suggest that connectivity over a spatial scale of 150km is possible between some source and sink populations. However, it appears unlikely that larvae from Northern Ireland will connect directly with sites on the Llŷn or Isle of Man. It also appears unlikely that larvae from the Llŷn connect directly to any of the other sites (Gormley *et al*., 2015). Inter-site differences in shell morphology, reflecting phenotypic differences have been observed between populations that relate to adaptation to local environmental conditions. Translocating individuals with ecophenotypes that are different to local populations may impact on the success of translocation may result in negative impacts on local populations through gene flow.

Introduction or spread of invasive non-indigenous species	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence.

Introduction of microbial pathogens	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

Brown & Seed (1977) reported a low level of infestation (ca 2%) 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 outbreaks 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 *Marteilia* 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.

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

Artisanal fisheries have targeted *Modiolus modiolus* as bait for the long-line 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). *Modiolus modiolus* is not currently directly targeted in the UK and hence this pressure is considered to be 'Not relevant'. While removal of commercially targeted species that are supported by *Modiolus* beds, such as scallops (*Aequipecten opercularis*), whelks (*Buccinum undatum*) and spider crabs (*Maja brachydactyla*) (Kent *et al*., 2017), will reduce species richness, the loss of targeted species is unlikely to adversely affect the *Modiolus modiolu*s bed through biological effects. The physical effects of dredging for scallops and other targeted species are discussed through the abrasion and penetration pressures. The removal of target species that predate on *Modiolus modiolus* would potentially be beneficial allowing the recruitment of juveniles to the adult population. However, such effects are not directly documented and could not be included in the assessment.

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

Removal of *Modiolus modiolus* within this biotope, as by-catch, will alter the physical structure of the biotope and reduce habitat complexity: these are considered ecological impacts and hence this biotope group is considered to be sensitive to this pressure, at the pressure benchmark. Epifauna associated with the bed is also likely to be damaged and removed as bycatch (Magorrian & Service, 1998) altering the structural complexity of the bed. A study by Garcia *et al*., (2006) found that by-catch constituted 28% (by weight) of the total catch of a dredge fishery for the scallop *Chlamys islandica*. *Modiolus modiolus* constituted 32% of the by-catch by biomass.

Sensitivity assessment. Resistance is assessed as 'Low' (damage or loss to 25-75% of the population), although the significance of the impact for the bed will depend on the spatial scale of the pressure footprint. Resilience is assessed as 'Low' (10-25 years), and sensitivity is assessed as 'High'. Epifauna associated with the bed is also likely to be damaged and removed.

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