



# MarLIN

## Marine Information Network

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

## Horse mussel (*Modiolus modiolus*)

MarLIN – Marine Life Information Network  
Biology and Sensitivity Key Information Review

Dr Harvey Tyler-Walters

2007-06-05

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/species/detail/1532>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

This review can be cited as:

Tyler-Walters, H., 2007. *Modiolus modiolus* Horse mussel. 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/marlin.sp.1532.2>



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](https://www.marlin.ac.uk). Based on a work at [www.marlin.ac.uk](https://www.marlin.ac.uk)

(page left blank)



Horse mussel bed with hydroids and red seaweed, Linga Sound, Shetland.

Photographer: Anon.

Copyright: Joint Nature Conservation Committee (JNCC)

See online review for  
distribution map

Distribution data supplied by the Ocean Biogeographic Information System (OBIS). To interrogate UK data visit the NBN Atlas.

<b>Researched by</b>	Dr Harvey Tyler-Walters	<b>Refereed by</b>	This information is not refereed.
<b>Authority</b>	(Linnaeus, 1758)		
<b>Other common names</b>	-	<b>Synonyms</b>	-

## Summary

### 🔍 Description

The shell is solid, swollen, approximately oblong or irregularly triangular in shape, with blunt umbones. The shell is dark blue or purple in colour, however the perisostracum gives adults a glossy yellow or dark brown appearance. In young animals the shell appears bluish and the periostracum is extended into long, smooth spines. The shell bears clear growth lines, and a sculpture of fine concentric lines and ridges. The inside of the shell is white, with a wide pallial line, a large anterior adductor muscle scar and small posterior adductor muscle scar. Adults are usually more than 10cm in length, although very large specimens may reach up to 22cm.

### 📍 Recorded distribution in Britain and Ireland

Found off all British coasts. Extensive beds are most common on northern or western coasts but absent south of the Irish Sea and Humber estuary. Records in the southwest and English Channel are likely to be single individuals or juveniles.

### 📍 Global distribution

Recorded from the White sea and Norway, off the Faroes and Iceland, south to the Bay of Biscay

and occasionally North Africa. Also from Labrador to North Carolina in the Atlantic and from the Bering Sea south to Japan and California in the Pacific.

### Habitat

Found part buried in soft sediments or coarse grounds or attached to hard substrata, forming clumps or extensive beds or reefs. May be found on the lower shore in rock pools or in laminarian holdfasts but more common subtidally to ca 280 m.

### ↓ Depth range

Lower intertidal to ca 280m.

### Q Identifying features

- Shell solid, swollen, equivalve and inequilateral.
- Shell approximately oblong to irregular triangular in shape.
- Shell margin smooth, and extended anteriorly of the beaks.
- Shell dark blue to purple with a glossy, yellow or dark brown periostracum in adults.
- Small (young) animals bluish in colour.
- Periostracum extended into long smooth spines in young.
- Beaks and umbones not quite anterior and blunt.
- Hinge line without teeth.
- Ligament external and deeply inset.
- Inside of shell white with a wide pallial line.
- Anterior adductor scar large, posterior scar small.

### Additional information

Distinguished from the common mussel (*Mytilus edulis*) by the blunter umbones, which are not quite anterior due to the extension of the shell margin in *Modiolus modiolus*.

### ✓ Listed by

### Further information sources

Search on:

    NBN WoRMS

## Biology review

### ☰ Taxonomy

Phylum	Mollusca	Snails, slugs, mussels, cockles, clams & squid
Class	Bivalvia	Clams, cockles, mussels, oysters, and scallops
Order	Mytilida	Mussels & crenellas
Family	Mytilidae	
Genus	Modiolus	
Authority	(Linnaeus, 1758)	
Recent Synonyms	-	

### 🌿 Biology

Typical abundance	High density
Male size range	35-200mm
Male size at maturity	
Female size range	Medium(11-20 cm)
Female size at maturity	
Growth form	Bivalved
Growth rate	See additional text
Body flexibility	None (less than 10 degrees)
Mobility	
Characteristic feeding method	Active suspension feeder
Diet/food source	
Typically feeds on	Bacteria, phytoplankton, detritus, and dissolved organic matter (DOM).
Sociability	
Environmental position	Epifaunal
Dependency	Independent.
Supports	Substratum The boring sponge <i>Cliona celata</i> and the pea crab <i>Pinnotheres</i> spp.
Is the species harmful?	No <i>Modiolus modiolus</i> beds have been exploited for food and as bait in Norwegian waters and on a lesser scale in Scottish waters (Comely, 1978; Holt <i>et al.</i> , 1998).

### 🏛️ Biology information

#### Typical abundance or density

Reported densities of horse mussel beds were relatively low (compared to common mussel beds) and variable, although grab samples and the interpretation of photographic images may be underestimates (Holt *et al.*, 1998). Reported densities include:

- 20-40 large individuals per m north of the Isle of Man (Holt *et al.*, 1998);
- 4-158 /m in Bay of Fundy, Nova Scotia (Wildish & Fader, 1998);

- 14.411.2 individuals/ m (Ojeda & Dearborn, 1989);
- 1-2/m in the intertidal and 37/m at 100m from the west coast of Scotland (Comely, 1978).

### Growth rates

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 45-60mm 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). The following growth rates have been reported:

- average lengths of 70mm or less reached at about 20 years of age in Firth of Lorne (Comely, 1978) and south east of the Isle of Man (Jasim, 1986);
- 35-40mm in length after 4-6 years (Anwar *et al.*, 1990);
- many populations reach 100mm at 12-18 years of age, e.g., west Scotland, Strangford Lough, and the Isle of Man (Comely, 1978, 1981; Jasim, 1986; Seed & Brown, 1975; Holt *et al.*, 1998).

Fast growing population of 10 year olds have been recorded on oil rigs in the North Sea (Holt *et al.*, 1998). Intertidal populations have been reported to be slow growing (Anwar *et al.*, 1990). Comely (1978) suggested that increased byssus production reduced growth rates in areas of loose sediment and/or strong currents. Comely (1978) also reported that a deep water population (200m) had reduced growth rates, possibly due to reduced food availability. Navarro & Thompson (1996) found that *Modiolus modiolus* in Newfoundland reduced its feeding activity in autumn and winter when food supply was poor but increased clearance rates and its absorption efficiency in spring in response to the spring phytoplankton bloom. Navarro & Thompson (1996) suggest that the horse mussel is adapted to survive in areas of intermittent food supply.

### Maturation

Sexual maturity occurs at about 35-40mm 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).

### Predators

Predators, largely crabs and starfish, play an important role in the population structure of horse mussel beds and determine the survival of juveniles to adulthood (Brown & Seed, 1977; Anwar *et al.*, 1990; Holt *et al.*, 1998). Predation probably also limits the ability of *Modiolus modiolus* to colonize other habitats, such as hard substrata, e.g. Sebens (1985) noted that *Asterias vulgaris* and *Buccinum undatum* predation removed juvenile *Mytilus* spp. and *Modiolus* spp. from vertical rock walls in the Gulf of Maine. Nielsen (1975) noted that *Modiolus* sp. occurred regularly in the stomach of *Buccinum undatum*. However, he concluded that the whelk probably fed on weak, or dead horse mussels, since when large horse mussels were threatened they either stayed shut long enough to deter the whelk, or if attacked could close their shell valves with enough force to break the shell lip of the whelk itself. Presumably juveniles are less able to defend themselves

## Parasites and diseases

Comely (1978) reported that ca 20% of older specimens, in an ageing population, were damaged or shells malformed by the boring sponge *Cliona celata*. 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.

## Habitat preferences

<b>Physiographic preferences</b>	Open coast, Offshore seabed, Strait / sound, Sea loch / Sea lough, Ria / Voe, Enclosed coast / Embayment
<b>Biological zone preferences</b>	Lower circalittoral, Lower eulittoral, Lower infralittoral, Sublittoral fringe, Upper circalittoral, Upper infralittoral
<b>Substratum / habitat preferences</b>	Artificial (man-made), Bedrock, Biogenic reef, Coarse clean sand, Fine clean sand, Gravel / shingle, Large to very large boulders, Mixed, Mud, Muddy gravel, Muddy sand, Rockpools, Sandy mud, Small boulders, Under boulders
<b>Tidal strength preferences</b>	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Strong 3 to 6 knots (1.5-3 m/sec.), Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
<b>Wave exposure preferences</b>	Moderately exposed, Sheltered, Very sheltered
<b>Salinity preferences</b>	Full (30-40 psu)
<b>Depth range</b>	Lower intertidal to ca 280m.
<b>Other preferences</b>	No text entered
<b>Migration Pattern</b>	Non-migratory / resident

## Habitat Information

*Modiolus modiolus* was also recorded as a dominant member of the species rich benthic assemblage found throughout the gravely sediments of St. George's Channel, and the outer regions of Cardigan Bay and Caernarfon Bay (Mackie *et al.*, 1995). Holt *et al.*, (1998; Table 1) lists the predominant forms of horse mussel beds in British waters.

## Habitat

*Modiolus modiolus* is adapted to live semi-infaunally with an endobysate 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* beds vary in size, density, thickness and form.

- Epifaunal horse mussels carpet steep surfaces and replace *Mytilus* spp. on offshore structures in cold waters, e.g., in Loch Duich, Loch Long and Loch Alsh (Holt *et al.*, 1998).
- Semi-infaunal reefs of large individuals about two-thirds embedded into sediment, forming an irregularly clumped layer and younger individuals between the byssal threads of larger individuals.
- Reefs form due to the build up of a mound of faecal mud and shell debris over several years. Reefs vary in size and height, depending on the build up of faecal mud and water flow rates. In strong tidal streams the beds may not retain the faecal mud and do not form raised beds (Holt *et al.*, 1998).
- On coarser grounds and in strong currents the horse mussels bind together the coarse sediment forming banks and live nested infaunally within the deposit.
- Coarse sediment banks formed by horse mussel beds form wave-like mounds or bioherms

in the Bay of Fundy up to 3m high and 20m wide and 10s -100s of metres in length, which are visible on sidescan sonar (Wildish *et al.*, 1998; Wildish & Fader, 1998). Similar banks, up to 1m high occur off the north east Isle of Man and Codling Bank, Ireland (Holt *et al.*, 1998).

- Horse mussel beds may occur as large and continuous banks (biogenic reefs) or as scattered clumps.
- Holt *et al.*, (1998) noted that extensive horse mussel beds or reefs were restricted to between 5 -50m in UK, although the large reefs recorded in the Bay of Fundy, Nova Scotia occurred at ca 80m (Wildish & Fader, 1998; Wildish *et al.*, 1998).

## Life history

### Adult characteristics

<b>Reproductive type</b>	Gonochoristic (dioecious)
<b>Reproductive frequency</b>	See additional information
<b>Fecundity (number of eggs)</b>	>1,000,000
<b>Generation time</b>	5-10 years
<b>Age at maturity</b>	3-8 years (see general biology)
<b>Season</b>	See additional text
<b>Life span</b>	20-100 years

### Larval characteristics

<b>Larval/propagule type</b>	-
<b>Larval/juvenile development</b>	Planktotrophic
<b>Duration of larval stage</b>	11-30 days
<b>Larval dispersal potential</b>	Greater than 10 km
<b>Larval settlement period</b>	Insufficient information

## Life history information

### Lifespan

Mussels over 25 years old are frequent in British populations, with occasional records of individuals of up to 35 years old. However, maximum ages are thought likely to be in excess of 50 years (Anwar *et al.*, 1990).

### Spawning

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

Recruitment is sporadic and highly variable seasonally, annually or with location (geographic and depth) (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).
- 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).

Comely (1978) suggested that recruitment was dependant on larvae from outside the area in areas of free water movement. 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. Therefore, recruitment is probably strongly affected by the local hydrographic regime.

### Post-settlement mortality

Widdows (1991) noted that in *Mytilus edulis* larvae any environmental factor that increased the larval development time (e.g. temperature or food availability) increased larval mortality. This is probably true for other mytilid larvae, such as *Modiolus modiolus*.

Pre- and post-settlement mortality is high due to predation. Settling larvae prefer the byssus threads and aggregations or clumps of adults which provide a refuge from predators. In infaunal populations, however, the byssal threads and clumps of adults will be less accessible, and predation risk higher as a result (Holt *et al.*, 1998). Most populations exhibit a bimodal size distribution of large, older specimens and small, younger specimens. Newly-settled horse mussels exhibit rapid growth prior to reaching maturity (see general biology), investing energy in growth rather than reproduction. Selection favours rapid growth to a size that is relatively immune to predation. Only the largest starfish and crabs can open mussels greater than 45-60mm and large horse mussels are thought to be largely predator free (Roberts, 1975; Seed & Brown, 1978; Holt *et al.*, 1998). Comely (1978) noted that *Modiolus modiolus* <40mm were rarely found away from large horse mussels.

## Sensitivity review

This MarLIN sensitivity assessment has been superseded by the MarESA approach to sensitivity assessment. MarLIN assessments used an approach that has now been modified to reflect the most recent conservation imperatives and terminology and are due to be updated by 2016/17.

### A Physical Pressures

	Intolerance	Recoverability	Sensitivity	Confidence
<b>Substratum Loss</b>	High	Low	High	Moderate
<p>Loss of substratum would cause removal of the resident population of horse mussels. Therefore, an intolerance of high has been recorded.</p> <p>Recovery would depend on recolonization from other populations. However, recruitment is sporadic, highly variable and some areas receive little or no recruitment for several years (see additional information below). Therefore, a recoverability of low has been recorded.</p>				
<b>Smothering</b>	Intermediate	Low	High	Very low
<p>Holt <i>et al.</i>, (1998) point out that the deposit of spoil or solid wastes (e.g. from capital dredging) that settle as a mass will smother any habitat it lands on. Biogenic reef formation involves the build up of faecal mud, suggesting that adults can move up through the accreting mud to maintain their relative position within the growing mound. Holt <i>et al.</i> (1998) note that there are no studies of the accretion rates that <i>Modiolus modiolus</i> beds can tolerate. Therefore, smothering by 5cm of sediment for a month (the benchmark level) is likely to remove a proportion of the population and an intolerance of intermediate has been recorded.</p> <p>Recruitment is sporadic, highly variable and some areas receive little or no recruitment for several years (see additional information below). Therefore, a recoverability of low has been recorded.</p>				
<b>Increase in suspended sediment</b>	Low	Immediate	Not sensitive	Low
<p><i>Modiolus modiolus</i> is found in a variety of turbid and clear water conditions (Holt <i>et al.</i>, 1998). Muschenheim &amp; Milligan (1998) noted that the height of the horse mussels beds in the Bay of Fundy positioned them within the region of high quality seston while avoiding high levels of re-suspended inorganic particulates (2.5-1500mg/l) at the benthic boundary layer. Comely (1978) noted that a population in a high turbidity area (up to 14mg/l inorganic suspended particulates) showed excessive pearl formation and poor shell growth and condition, although the populations poor condition was probably partly due to old age and senility. Therefore, although high levels of suspended sediment may interrupt feeding, or result in the production of pseudofaeces at energetic cost, <i>Modiolus modiolus</i> is probably able to tolerate increases in suspended sediment for intervals equivalent to the benchmark and an intolerance of low has been recorded. Increases in organic suspended particulates may increase food availability and be beneficial. <i>Modiolus modiolus</i> is adapted to a benthic sediment habitat and is probably capable of rejecting excess silt or particulates, therefore a recoverability of 'immediate' has been recorded.</p>				
<b>Decrease in suspended sediment</b>	Low	Immediate	Not sensitive	Low
<p>A decrease in suspended sediment may decrease the food availability for <i>Modiolus modiolus</i>. However, Navarro &amp; Thompson, (1996) demonstrated that <i>Modiolus modiolus</i> was adapted to seasonal fluctuations in food availability, reducing feeding activity in winter and increasing</p>				

feeding activity during the summer phytoplankton bloom, for which it had a high absorption efficiency. Therefore, *Modiolus modiolus* is unlikely to be adversely affected by a decrease in suspended sediment for a month (see benchmark).

#### Desiccation

High

Low

High

High

On exposure to air, *Modiolus modiolus* closed its shell initially, but after a few minutes to a few hours the shell valves gape. As a result the mantle fluid drains away, leaving the tissue susceptible to evaporation and desiccation (Coleman, 1973). Coleman (1973) estimated that death occurred after 30-40% water loss from the tissue, which was achieved after 1 hr in moving air. Individuals lost up to 80% of tissue water after 6 hrs emersion. Coleman (1973) concluded that *Modiolus modiolus* may not die if exposed to still air for 2-3 days (depending on temperature), but in moving air death would be rapid. However, Kanwisher (1955; cited in Coleman, 1973) suggested that *Modiolus* could withstand up to 65% water loss if the water was removed as ice, i.e. at low temperatures. Therefore, *Modiolus modiolus* is unable to control its gape, and shows poor adaptation to aerial exposure, which probably explains its restricted distribution in the intertidal, being limited to lower shore rockpools and areas of high humidity and low air movement. *Modiolus modiolus* is probably very intolerant of an increase in desiccation and, therefore, an intolerance of high has been recorded.

Recovery would depend on recolonization from other populations. However, recruitment is sporadic, highly variable and some areas receive little or no recruitment for several years (see additional information below). Therefore, a recoverability of low has been recorded.

#### Increase in emergence regime

High

Low

High

Moderate

Davenport & Kjørsvik (1982) suggested that *Modiolus modiolus* was poorly adapted to life in the intertidal due to its patent byssal opening, inability to control its shell gape, thin shell, lack of mobility and restricted thermal tolerance. In addition, increased emergence will increase the risk of desiccation. The majority of populations are subtidal, however intertidal populations or shallow subtidal populations occasionally exposed at extreme low water may be vulnerable to increased emergence and hence, exposure to desiccation and temperature extremes. Therefore, an intolerance of high has been recorded.

Recovery would depend on recolonization from other populations. However, recruitment is sporadic, highly variable and some areas receive little or no recruitment for several years (see additional information below). Therefore, a recoverability of low has been recorded.

#### Decrease in emergence regime

Tolerant\*

Not relevant

Not sensitive\*

Not relevant

Decreased emergence is unlikely to adversely affect populations and may even allow the populations to feed longer and improve condition, i.e. they may benefit from decreased emergence.

#### Increase in water flow rate

Intermediate

Low

High

Low

Holt *et al.* (1998) suggested that water movement was an important factor in the build up of the denser reefs and beds of *Modiolus modiolus*, since the denser reefs were found in areas of moderate to strong tidal currents. Wildish *et al.* (2000) examined suspension feeding in horse mussels in a flume and noted that they kept both the exhalent and inhalent siphons open over the range of flow rates studied, 12-63 cm/sec (approximates to weak to moderately strong tidal streams). However, the inhalent siphon closed by about 20% in currents above 55 cm/sec. The horse mussel reefs or bioherms observed in the Bay of Fundy were arranged parallel to flow within the Bay (Wildish & Fader, 1998; Wildish *et al.*, 1998). *Modiolus modiolus* populations are found from weak to strong tidal streams and are, therefore, probably tolerant of changes in water flow within this range. However, Comely (1978) suggested that areas exposed strong currents required an increase in byssus production, at energetic cost, and

resulted in lower growth rates. Populations in strong tidal streams may be more intolerant of an increase in water flow. Fouling by epifauna and algae may also increase the populations intolerance 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. Exposure to very strong water flow may also result in loss of individuals due to the removal of the substratum. Therefore, intolerance to increased water flow is dependant on the nature of the substratum and the level of epifaunal or epifloral fouling and an intolerance of intermediate has been recorded.

Recruitment is sporadic, highly variable and some areas receive little or no recruitment for several years (see additional information below). Therefore, a recoverability of low has been recorded.

#### Decrease in water flow rate

Intermediate

Low

High

Moderate

Muschenheim & Milligan (1998) noted that horse mussel beds in the Bay of Fundy occurred in transitional, well mixed waters, so that the beds were supplied with high quality seston (organic particulates and phytoplankton) from the euphotic zone. They also suggested that beds in areas of moderate current flow and/or a greater depths were not exposed to high concentrations of suspended inorganic particulates, which would otherwise dilute out the high quality seston (food). However, flume experiments suggest that *Modiolus* sp. can deplete the seston directly over dense beds when water flow is low, resulting in a reduction in the density of the mussel bed (Wildish & Kristmanson, 1984, 1985; Holt *et al.*, 1998). Therefore, an intolerance of intermediate has been recorded. Holt *et al.*, 1998 note that no comparable studies has been found on British *Modiolus* sp. populations.

Populations already present in areas of weak water flow may also be exposed to increased siltation (see above) and the risk of deoxygenation (see below).

Recruitment is sporadic, highly variable and some areas receive little or no recruitment for several years (see additional information below). Therefore, a recoverability of low has been recorded.

#### Increase in temperature

Intermediate

Low

High

Very low

*Modiolus modiolus* is a boreal species reaching its southern limit in British waters (Holt *et al.*, 1998). Davenport & Kjørsvik (1982) suggested that its inability to tolerate temperature change was a factor preventing the horse mussel from colonizing the intertidal in the UK. Intertidal specimens were more common on northern Norwegian shores (Davenport & Kjørsvik, 1982). Little information on temperature tolerance in *Modiolus modiolus* was found, however, its upper lethal temperature is lower than that for *Mytilus edulis* (Bayne *et al.*, 1976b) 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* reaches its southern limit in British waters it may be susceptible to long term increases in summer water temperatures.

Therefore, the absence of this species from the intertidal in the UK (with a few exceptions) and its predominantly northern distribution suggests that it is intolerant of temperature change. The suggested susceptibility to long-term summer temperature rise could result in a reduction in the extent of the UK population. Therefore, an intolerance of intermediate has been recorded.

Recruitment is sporadic, varies with season, annually and with location and hydrographic regime and is generally low, therefore it may take many years for a population to recover from damage and a recoverability of low (10-25years) has been recorded.

#### Decrease in temperature

Tolerant\*

Not relevant

Not sensitive\*

Low

*Modiolus modiolus* is a boreal species reaching its southern limit in British waters (Holt *et al.*, 1998). Although no information on its lower temperature tolerance was found its northern distribution suggest that it would probably tolerate a decrease of average winter sea temperatures in the UK (Holt *et al.*, 1998; Davenport & Kjørsvik 1982) but may increase in abundance and extent. Therefore, *Modiolus modiolus* has been ranked as 'tolerant\*' to decreased temperatures.

**Increase in turbidity**                      **Low**                      **Very high**                      **Very Low**                      **Moderate**

*Modiolus modiolus* is found in a wide range of turbid to clear waters (Holt *et al.*, 1998). Increased turbidity may decrease phytoplankton primary productivity and hence the food supply for the horse mussel. However, Navarro & Thompson (1996) concluded that the horse mussel was adapted to an intermittent and often inadequate food supply. Therefore, an intolerance of low has been recorded.

Once conditions return to normal it is likely that the population will take time to recover condition, therefore a recoverability of very high has been recorded.

**Decrease in turbidity**                      Tolerant\*                      Not relevant                      Not sensitive\*

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

**Increase in wave exposure**                      Intermediate                      Low                      High                      Very low

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. *Mytilus edulis* was shown to increase byssus production in response to agitation (Young, 1985) and *Modiolus modiolus* may respond similarly. However, horse mussels attached to hard substrata are probably more intolerant of wave action than *Mytilus edulis* due to their larger size, and hence increased drag. 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. In addition, shallow subtidal populations are found in sheltered conditions (e.g. Strangford Lough) rather than wave exposed conditions. Therefore, it is likely that an increase in wave action will result in loss of a proportion of the population and an intolerance of intermediate has been recorded. Shallow subtidal *Modiolus modiolus* beds may be more intolerant of prolonged change or storms.

Recruitment is sporadic, highly variable and some areas receive little or no recruitment for several years (see additional information below). Therefore, a recoverability of low has been recorded.

**Decrease in wave exposure**                      Tolerant\*                      Not relevant                      Not sensitive\*

Tidal flow rather than wave action is the predominant force in feeding, so that wave action is most important in relation to the potential destruction of beds. Providing that tidal flows remains reasonably strong, horse mussel beds may benefit from a reduction in wave action and a rank of 'tolerant\*' is suggested. 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.

**Noise**                      Tolerant                      Not relevant                      Not sensitive                      High

*Modiolus modiolus* can probably detect vibrations but is relatively immobile, and unlikely to be adversely affected by noise.



**Visual Presence** Tolerant Not relevant Not sensitive High

*Modiolus modiolus* can probably detect changes in light intensity, however, it is unlikely to be adversely affected by visual presence and shading at the level of the benchmark.

**Abrasion & physical disturbance** High Low High Low

*Modiolus modiolus* are large and relatively tough. Holt *et al.* (1998) suggested that horse mussels beds were not particularly fragile, even when epifaunal, with semi-infaunal and infaunal population being less vulnerable to physical disturbance. Clumps of horse mussels on muddy substrata may be more intolerant. However, impacts from towed fishing gear (e.g. scallop dredges) are known to flatten clumps and aggregations, and may break off sections of raised reefs and probably damage individual mussels (Holt *et al.*, 1998). The shells of older specimens can be very brittle due to infestations of the boring sponge *Cliona celata* (Comely, 1978; Holt *et al.*, 1998). Although scallop or queen scallop dredging was probably not viable over rough ground such as horse mussel beds, it was suggested that scallop dredging on areas adjacent to beds in the south east of the Isle of Man had 'nibbled away at the edges' of dense beds, which had become less dense and more scattered (Holt *et al.*, 1998). Extensive beds were present in the north of the Isle of Man where scallop dredging has apparently not occurred (Holt *et al.*, (1998). 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; Service 1998). Holt *et al.* (1998) suggested that damage by whelk potting was not likely to be severe but noted that epifaunal populations may be more intolerant Overall, an intolerance of high has been recorded. Recruitment is sporadic, varies with season, annually, with location, and hydrographic regime, and is generally low, therefore it may take many years for a population to recover from damage, and a recoverability of low (10-25 years) has been recorded

**Displacement** Low Very high Very Low Very low

Holt *et al.*, (1998) noted the survival of clumps torn from a horse mussel bed was not known. *Modiolus modiolus* displaced from the beds will probably be able to re-attach to suitable substratum using their byssus threads, although no information was found concerning their ability to burrow. Therefore, an intolerance of low has been recorded, albeit with very low evidence/confidence. The ability of clumps or individuals to maintain a viable population will depend on the location and depth of the new habitat, food supply, and the local hydrographic regime.

## Chemical Pressures

**Synthetic compound contamination** Intolerance Recoverability Sensitivity Confidence

No information concerning the effects of synthetic contaminants on *Modiolus modiolus* was found. However, it is likely to have a similar metabolism to that of *Mytilus edulis* and hence, possibly, a similar tolerance to chemical contaminants.

Livingstone & Pipe (1992) cite Palmork & Solbakken (1981) who reported that *Modiolus modiolus* accumulated poly-aromatic hydrocarbons (PAHs) and examined the depuration of phenanthrene from horse mussel tissue. However, no effects on the horse mussel were documented. PAHs contribute to a reduced scope for growth in *Mytilus edulis* (Widdows *et al.*, 1995) and probably have a similar effect in the horse mussel but to an unknown degree.

Tri butyl-tin (TBT) has been reported to affect bivalve mollusc as follows: reduced spatfall in *Pecten maximus*, *Musculus marmoratus* and *Limaria hians*; inhibition of growth in *Mytilus edulis* larvae, and inhibition of growth and metamorphosis in *Mercenaria mercenaria* larvae (Bryan & Gibbs, 1991).

Therefore, it is likely that TBT may interfere with growth and settlement of *Modiolus modiolus* larvae. Horse mussel population exhibit sporadic recruitment, therefore any factor that adversely affect recruitment will have an adverse effect on the population, although the effects may not be observed for some time since the species is so long lived. Therefore, an intolerance of intermediate has been recorded albeit at very low confidence.

Recruitment is sporadic, varies with season, annually and with location and hydrographic regime and is generally low, therefore it may take many years for a population to recover from damage and a recoverability of low (10-25years) has been recorded.

#### Heavy metal contamination

Low

Very high

Very Low

Very low

*Modiolus modiolus* may exhibit tolerance to heavy metals similar to that of *Mytilus edulis*.

The tissue distribution of Cd, Zn, Cu, Mg, Mn, Fe and Pb was examined in *Modiolus modiolus* by Julshamn & Andersen (1983) who reported the presence of Cd binding proteins but did not document any adverse effects. Richardson *et al.* (2001) examined the presence of Cu, Pb and Zn in the shells of *Modiolus modiolus* from a relatively un-contaminated site and from a site affected by sewage sludge dumping. The persistence of a population of horse mussels at the sewage sludge dumping site suggests tolerance to heavy metal contamination levels at that site. Holt *et al.* (1998) reported that long-term changes in contaminant loads associated with spoil dumping were detectable in the shells of horse mussels in a bed off the Humber estuary. This observation showed survival of horse mussels in the vicinity of a spoil dumping ground but no information on their condition was available (Holt *et al.*, 1998).

Overall, therefore, horse mussels may show a similar tolerance to heavy metals as *Mytilus edulis* but in the absence of any evidence of mortalities an intolerance of low has been recorded. On return to un-contaminated conditions, removal or depuration of heavy metals may take some time and a recoverability of very high has been recorded.

#### Hydrocarbon contamination

Low

Very high

Very Low

Low

Horse mussels are protected from the direct effects of oil spills due to their subtidal habitat, although shallow subtidal and intertidal populations will be more vulnerable. Horse mussels may still be affected by oil spills and associated dispersants where the water column is well mixed vertically, e.g. in areas of strong wave action. Oils may be ingested as droplets or adsorbed onto particulates. Hydrocarbons may be ingested or absorbed from particulates or in solution, especially PAHs.

Suchanek (1993) noted that sub-lethal levels of oil or oil fractions reduce feeding rates, reduce respiration and hence growth, and may disrupt gametogenesis in bivalve molluscs. Widdows *et al.* (1995) noted that the accumulation of PAHs contributed to a reduced scope for growth in *Mytilus edulis*.

Holt & Shalla (unpublished; cited in Holt *et al.*, 1998) did not observe any visible effects on a population of *Modiolus modiolus* within 50 m of the wellhead of a oil/gas exploration rig (using water based drilling muds) in the north east of the Isle of Man. May & Pearson (1995) reviewed the effects of the oil industry on the macrobenthos of Sullom Voe. They reported that stations in the vicinity of ballast water diffuser, probably containing fresh petrogenic hydrocarbons, showed a consistently high diversity (since surveys started in 1978) and included patches of *Modiolus beds*. The strong currents in the area probably flushed polluting materials away from the station, and hence reduced the stress on the population (May & Pearson, 1995). However, it is possible that hydrocarbon contamination may reduce

reproductive success and growth rates in horse mussel populations. Reduced scope for growth may be of particular importance in juveniles that are subject to intense predation pressure, resulting in fewer individuals reaching breeding age.

However, the long term persistence of a diverse bed of *Modiolus* sp. in the vicinity of a hydrocarbon contaminated effluent suggests an intolerance of low.

Recruitment is sporadic and variable (see additional information below), therefore it may take many years for a population to recover from damage and a recoverability of low (10-25years) has been recorded.

#### Radionuclide contamination

Not relevant

Not relevant

Insufficient information

#### Changes in nutrient levels

Low

Very high

Very Low

Low

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. Therefore, a rank of 'tolerant\*' has been recorded. 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 out-breaks of paralytic shellfish poisoning in which bivalves accumulate toxins from algal blooms, although a direct causal effect required further research.

Therefore, an intolerance of low (at the benchmark level) has been recorded due to the potential sub-lethal effects of algal blooms. A recoverability of very high has been recorded to represent the time required for algal toxins to be depurated from horse mussels.

#### Increase in salinity

Not relevant

Not relevant

Not relevant

Not relevant

*Modiolus modiolus* was considered to be poorly adapted to fluctuating salinities, due to its patent byssal aperture and restricted salinity tolerance (Bayne *et al.*, 1976b). Pierce (1970) exposed *Modiolus* sp. to range of salinities between 1.5 and 54psu and reported that *Modiolus modiolus* survived for 21 days (the duration of the experiment) between 27 and 41psu.

However, the majority of *Modiolus modiolus* populations are subtidal and therefore, unlikely to be exposed to salinities above that of full seawater. Only intertidal populations in rock pools or populations exposed to hypersaline effluents are likely to experience increased salinity.

#### Decrease in salinity

High

Low

High

Moderate

*Modiolus modiolus* was considered to be poorly adapted to fluctuating salinities, due to its patent byssal aperture and restricted salinity tolerance (Bayne *et al.*, 1976b). Pierce (1970) exposed *Modiolus* sp. 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. 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. Davenport & Kjørsvik (1982) also reported that Shumway (1977) had found the horse mussels tolerated simulated tidal fluctuations between full seawater and fresh



water. Shumway (1977) reported that *Modiolus modiolus* survived for 10 days exposed to either gradual or sudden cyclic changes in salinity between 50 and 100% seawater. In addition, Shumway (1977) reported that the salinity of the mantle fluid changed only gradually and Piece (1970) noted that the body fluid remained hyperosmotic to the environment, suggesting that diffusion through the byssal aperture was slow (Shumway, 1977; Davenport & Kjörsvik 1982). Holt *et al.* (1998) note that young *Modiolus* occasionally occur subtidally in estuaries. Therefore, the horse mussel will probably survive short term exposure to reduced salinity conditions.

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.). Therefore, an intolerance of high has been recorded.

Recruitment is sporadic, varies with season, annually and with location and hydrographic regime and is generally low, therefore it may take many years for a population to recover from damage and a recoverability of low (10-25years) has been recorded.

### Changes in oxygenation Low      Very high      Very Low      Moderate

Theede *et al.* (1969) examined the relative tolerance of gill tissue from several species of bivalve to exposure to 0.21mg/l O<sub>2</sub> with or without 6.67mg of sulphide (at 10°C and 30psu). *Modiolus modiolus* tissue was found to be the most resistant of the species studied, retaining some ciliary activity after 120hrs compared with 48hrs for *Mytilus edulis*. While it is difficult to extrapolate from tissue resistance to whole animal resistance (taking into account behavioural adaptations such as valve closure) this 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, an intolerance of low has been recorded at the benchmark level.

Anaerobic metabolism often results in an oxygen debt and individuals may have to make up for energy reserves depleted during hypoxia, therefore a recoverability of very high has been recorded.

## Biological Pressures

	Intolerance	Recoverability	Sensitivity	Confidence
<b>Introduction of microbial pathogens/parasites</b>	Low	Very high	Very Low	Low

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. Therefore, an intolerance of low was recorded.

<b>Introduction of non-native species</b>	Not relevant	Not relevant
---	--------------	--------------

No information concerning the effects of competition with non-native or alien species was found.

<b>Extraction of this species</b>	High	Low	High	Moderate
-----------------------------------	------	-----	------	----------

Holt *et al.* (1998) reported that, although there was no large scale horse mussel fishery in the United Kingdom, there have been small scale local fisheries in Scotland for food or bait and

that horse mussels were occasionally seen on markets in Lancashire. Holt *et al.* suggest that any direct fishery would be very damaging. Therefore, extraction of 50% of the population (the benchmark level) would result in an intolerance of intermediate. However, extraction of 50% of a horse mussel bed may result in further dislodgement of clumps of mussels, and adversely affect subsequent juvenile survival and hence recovery, since juveniles require the presence of adults to shelter from predators. Therefore, an intolerance of high has been recorded. Recruitment is sporadic, variable and is generally low, therefore it may take many years for a population to recover from damage and a recoverability of low (10-25years) has been recorded.

### Extraction of other species

Intermediate

Low

High

High

Impacts from towed fishing gear (e.g. scallop dredges) are known to flatten clumps and aggregations and may break off sections of raised reefs and probably damage individual mussels (Holt *et al.*, 1998). The shells of older specimens can be very brittle due to infestations of the boring sponge *Cliona celata* (Comely, 1978; Holt *et al.*, 1998). It was suggested that scallop dredging on areas adjacent to beds in the south east of the Isle of Man had 'nibbled away at the edges' of denser beds, which had become less dense and more scattered (Holt *et al.*, 1998). Veale *et al.* (2000) reported that the total abundance, biomass and production of the major taxa studied, including *Modiolus modiolus*, decreased with increasing scallop fishing effort in the south of the Isle of Man. Magorrian & Service (1998) reported that queen scallop trawling resulted in flattening of the horse mussel bed, disruption of clumps of horse mussels and removal of emergent epifauna in Strangford Lough and were able to identify different levels of impact to the horse mussel bed from impacted but largely intact to few *Modiolus modiolus* intact with lots of shell debris (Service & Magorrian, 1997; Magorrian & Service, 1998; Service 1998).

Overall, dredging for scallops is likely to result in disruption of the horse mussel beds and loss of a proportion of the population in the short term. However, the horse mussel beds may be more intolerant in the long-term, depending on the level of fishing effort. Therefore an intolerance of high has been recorded.

Recruitment is sporadic, variable and is generally low, therefore it may take many years for a population to recover from damage and a recoverability of low (10-25years) has been recorded.

## Additional information

### Recoverability

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, see reproduction) (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.).

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) cleared 115cm<sup>2</sup> 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 life span 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.

## Importance review

### Policy/legislation

### ★ Status

National (GB) importance	Not rare/scarce	Global red list (IUCN) category	-
--------------------------	-----------------	---------------------------------	---

### Non-native

Native	-	Date Arrived	Not relevant
Origin	-		

### Importance information

- Clumps or beds of *Modiolus modiolus* significantly modify the habitat, increasing habitat complexity and forming raised beds that may be visible on side-scan sonar (Wildish & Fader, 1998; Wildish *et al.*, 1998; Holt *et al.*, 1998; Magorrian & Service, 1998).
- Horse mussel beds provide a habitat for a rich assemblage of species, including most of the major groups of organisms (see the review of MCR.ModT for further information) (Holt *et al.*, 1998).
- *Modiolus modiolus* beds support populations of many other suspension feeders and may be very extensive. Horse mussels beds may deplete seston concentrations when water flow is low (Wildish & Kristmanson, 1994, 1995). However, filter feeding by horse mussel beds may be of great importance in channelling primary phytoplankton productivity to the benthos, termed 'benthic-pelagic' coupling. Navarro and 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).
- *Modiolus modiolus* beds are included as a Habitat Action Plan under the UK Biodiversity Action Plan (Anonymous, 1999u).
- *Modiolus modiolus* beds may be protected under the Habitats Directive within the Annex I habitats 'Reefs' and 'Large shallow inlets and bays' and potentially within the habitat 'Estuaries' (Jones *et al.*, 2000).
- Service (1998) suggested limits of acceptable change for horse mussel populations in Strangford Lough, but noted that further research was required to derive ecological quality standards.

## Bibliography

- Anonymous, 1999u. *Modiolus modiolus* beds. Habitat Action Plan. In *UK Biodiversity Group. Tranche 2 Action Plans. English Nature for the UK Biodiversity Group, Peterborough., English Nature for the UK Biodiversity Group, Peterborough.*
- 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.
- 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. & Gibbs, P.E., 1991. Impact of low concentrations of tributyltin (TBT) on marine organisms: a review. In: *Metal ecotoxicology: concepts and applications* (ed. M.C. Newman & A.W. McIntosh), pp. 323-361. Boston: Lewis Publishers Inc.
- Coleman, N., 1973. Water loss from aerially exposed mussels. *Journal of Experimental Marine Biology and Ecology*, **12**, 145-155.
- Comely, C.A., 1978. *Modiolus modiolus* (L.) from the Scottish West coast. I. Biology. *Ophelia*, **17**, 167-193.
- Comely, C.A., 1981. The physical and biological condition of *Modiolus modiolus* (L.) in selected Shetland voes. *Proceedings of the Royal Society of Edinburgh, Series B*, **80**, 299-321.
- Davenport, J. & Kjörsvik, E., 1982. Observations on a Norwegian intertidal population of the horse mussel *Modiolus modiolus* (L.). *Journal of Molluscan Studies*, **48**, 370-371.
- 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.
- Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore*. Cambridge: Cambridge University Press.
- Hayward, P., Nelson-Smith, T. & Shields, C. 1996. *Collins pocket guide. Sea shore of Britain and northern Europe*. London: HarperCollins.
- Henderson, J.T., 1929. Lethal temperatures of *Lamellibranchiata*. *Contributions to Canadian Biology and Fisheries*, **4**, 395-412.
- Hiscock, K., 1983. Water movement. In *Sublittoral ecology. The ecology of shallow sublittoral benthos* (ed. R. Earll & D.G. Erwin), pp. 58-96. Oxford: Clarendon Press.
- 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.
- Howson, C.M. & Picton, B.E., 1997. *The species directory of the marine fauna and flora of the British Isles and surrounding seas*. Belfast: Ulster Museum. [Ulster Museum publication, no. 276.]
- 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.
- 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>
- Julshamn, K. & Andersen, K-J., 1983. Subcellular distribution of major and minor elements in unexposed molluscs in western Norway-III. The distribution and binding of .....in the kidney and the digestive system of the horse mussel *Modiolus modiolus*. *Comparative Biochemistry and Physiology*, **75A**, 17-20.
- Livingstone, D.R. & Pipe, R.K., 1992. Mussels and environmental contaminants: molecular and cellular aspects. In *The mussel Mytilus: ecology, physiology, genetics and culture*, (ed. E.M. Gosling), pp. 425-464. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]
- Mackie, A.S.Y., Oliver, P.G. & Rees, E.I.S., 1995. Benthic biodiversity in the southern Irish Sea. *Studies in Marine Biodiversity and Systematics from the National Museum of Wales. BIOMOR Reports*, no. 1.
- Magorrian, B.H. & Service, M., 1998. Analysis of underwater visual data to identify the impact of physical disturbance on horse mussel (*Modiolus modiolus*) beds. *Marine Pollution Bulletin*, **36**, 354-359.
- May, S.J. & Pearson, T.H., 1995. Effects of oil-industry operations on the macrobenthos of Sullom Voe. *Proceedings of the Royal Society of Edinburgh*, **103B**, 69-97.
- Muschenheim, D.K. & Milligan, T.G., 1998. Benthic boundary level processes and seston modification in the Bay of Fundy (Canada). *Vie et milieu, Paris*, **48**, 285-294.
- 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.

- Navarro, J.M. & Thompson, R.J., 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dillwyn) during the spring diatom bloom. *Journal of Experimental Marine Biology and Ecology*, **209**, 1-13.
- Nielsen, C., 1975. Observations on *Buccinum undatum* L. attacking bivalves and prey responses with a short review on attack methods of other prosobranchs. *Ophelia*, **13**, 87-108.
- Næs, K., Oug, E. & Knutzen, J., 1998. Source and species-dependant accumulation of polycyclic aromatic hydrocarbons (PAHs) in littoral indicator organisms from Norwegian smelter-affected marine waters. *Marine Environmental Research*, **45**, 193-207.
- Ojeda, F.P. & Dearborn, J.H., 1989. Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine: seasonal and bathymetric distribution. *Marine Ecology Progress Series*, **57**, 147-161.
- Pierce, S.K., 1970. The water balance of *Modiolus* (Mollusca: Bivalvia: Mytilidae): osmotic concentrations in changing salinities. *Comparative Biochemistry and Physiology*, **36**, 521-533.
- 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.
- Roberts, D., 1975. Sub-lethal effects of chlorinated hydrocarbons on bivalves. *Marine Pollution Bulletin*, **6**, 20-24.
- Rowell, T.W., 1967. *Some aspects of the ecology, growth and reproduction of the horse mussel Modiolus modiolus*, MSc Thesis. Queens' University, Ontario
- Sebens, K.P., 1985. Community ecology of vertical rock walls in the Gulf of Maine: small-scale processes and alternative community states. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.* (ed. P.G. Moore & R. Seed), pp. 346-371. London: Hodder & Stoughton Ltd.
- Seed, R. & Brown, R.A., 1975. The influence of reproductive cycle, growth, and mortality on population structure in *Modiolus modiolus* (L.), *Cerastoderma edule* (L.) and *Mytilus edulis* L. (Mollusca: Bivalvia). In *Proceedings of the 9th European Marine Biology Symposium, Dunstaffnage Marine Laboratory, Oban, 2-8 October, 1974*, (ed. H. Barnes), pp. 257-274.
- 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.
- Seed, R., 1976. Ecology. In *Marine mussels: their ecology and physiology*, (ed. B.L. Bayne), pp. 81-120. Cambridge: Cambridge University Press.
- Service, M. & Magorrian, B.H., 1997. The extent and temporal variation of disturbance to epibenthic communities in Strangford Lough, Northern Ireland. *Journal of the Marine Biological Association of the United Kingdom*, **77**, 1151-1164.
- Service, M., 1998. Recovery of benthic communities in Strangford Lough following changes in fishing practice. *ICES Council Meeting Paper*, CM 1998/V.6, 13pp., Copenhagen: International Council for the Exploration of the Sea (ICES).
- Shumway, S.E., 1977. Effect of salinity fluctuations on the osmotic pressure and Na<sup>+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> 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.
- Suchanek, T.H., 1985. Mussels and their role in structuring rocky shore communities. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.*, (ed. P.G. Moore & R. Seed), pp. 70-96.
- Suchanek, T.H., 1993. Oil impacts on marine invertebrate populations and communities. *American Zoologist*, **33**, 510-523.
- Tebble, N., 1976. *British Bivalve Seashells. A Handbook for Identification*, 2nd ed. Edinburgh: British Museum (Natural History), Her Majesty's Stationary Office.
- Veale, L.O., Hill, A.S., Hawkins, S.J. & Brand, A.R., 2000. Effects of long term physical disturbance by scallop fishing on subtidal epifaunal assemblages and habitats. *Marine Biology*, **137**, 325-337.
- Wiborg, F.K., 1946. Undersøkelser over oskallet (*Modiolus modiolus* (L.)). *Fiskeridirektoratets Skrifter (ser. Havundersøkelser)*, **8**, 85.
- Widdows, J., Donkin, P., Brinsley, M.D., Evans, S.V., Salkeld, P.N., Franklin, A., Law, R.J. & Waldock, M.J., 1995. Scope for growth and contaminant levels in North Sea mussels *Mytilus edulis*. *Marine Ecology Progress Series*, **127**, 131-148.
- 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., 1984. Importance of mussels of the benthic boundary layer. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1618-1625.
- Wildish, D.J. & Kristmanson, D.D., 1985. Control of suspension feeding bivalve production by current speed. *Helgolander Meeresuntersuchungen*, **39**, 237-243.
- Wildish, D.J., Akage, H.M. & Hamilton, N., 2000. Effects of velocity on horse mussel initial feeding behaviour. *Canadian Technical Report of Fisheries and Aquatic Sciences*, no. 2325, 34pp.
- 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.
- Witman, J.D., 1984. *Ecology of rocky subtidal communities: the role of Modiolus modiolus (L.) and the influence of disturbance, competition and mutualism*, Ph.D. thesis. University of New Hampshire, Durham, USA.
- Young, G.A., 1985. Byssus thread formation by the mussel *Mytilus edulis*: effects of environmental factors. *Marine Ecology Progress*

Series, 24, 261-271.

## Datasets

Centre for Environmental Data and Recording, 2018. Ulster Museum Marine Surveys of Northern Ireland Coastal Waters. Occurrence dataset <https://www.nmni.com/CEDaR/CEDaR-Centre-for-Environmental-Data-and-Recording.aspx> accessed via NBNAtlas.org on 2018-09-25.

Conchological Society of Great Britain & Ireland, 2018. Mollusc (marine) data for Great Britain and Ireland - restricted access. Occurrence dataset: <https://doi.org/10.15468/4bsawx> accessed via GBIF.org on 2018-09-25.

Conchological Society of Great Britain & Ireland, 2018. Mollusc (marine) data for Great Britain and Ireland. Occurrence dataset: <https://doi.org/10.15468/aurwcz> accessed via GBIF.org on 2018-09-25.

Environmental Records Information Centre North East, 2018. ERIC NE Combined dataset to 2017. Occurrence dataset: <http://www.ericnortheast.org.uk/home.html> accessed via NBNAtlas.org on 2018-09-38

Fenwick, 2018. Aphotomarine. Occurrence dataset <http://www.aphotomarine.com/index.html> Accessed via NBNAtlas.org on 2018-10-01

Kent Wildlife Trust, 2018. Kent Wildlife Trust Shoresearch Intertidal Survey 2004 onwards. Occurrence dataset: <https://www.kentwildlifetrust.org.uk/> accessed via NBNAtlas.org on 2018-10-01.

Merseyside BioBank., 2018. Merseyside BioBank (unverified). Occurrence dataset: <https://doi.org/10.15468/iou2ld> accessed via GBIF.org on 2018-10-01.

National Trust, 2017. National Trust Species Records. Occurrence dataset: <https://doi.org/10.15468/opc6g1> accessed via GBIF.org on 2018-10-01.

NBN (National Biodiversity Network) Atlas. Available from: <https://www.nbnatlas.org>.

Norfolk Biodiversity Information Service, 2017. NBIS Records to December 2016. Occurrence dataset: <https://doi.org/10.15468/jca5lo> accessed via GBIF.org on 2018-10-01.

OBIS (Ocean Biogeographic Information System), 2019. Global map of species distribution using gridded data. Available from: Ocean Biogeographic Information System. [www.iobis.org](http://www.iobis.org). Accessed: 2019-03-21

Outer Hebrides Biological Recording, 2018. Invertebrates (except insects), Outer Hebrides. Occurrence dataset: <https://doi.org/10.15468/hpavud> accessed via GBIF.org on 2018-10-01.

South East Wales Biodiversity Records Centre, 2018. SEWBReC Molluscs (South East Wales). Occurrence dataset: <https://doi.org/10.15468/jos5ga> accessed via GBIF.org on 2018-10-02.