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Cerastoderma edule and polychaetes in littoral muddy sand

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

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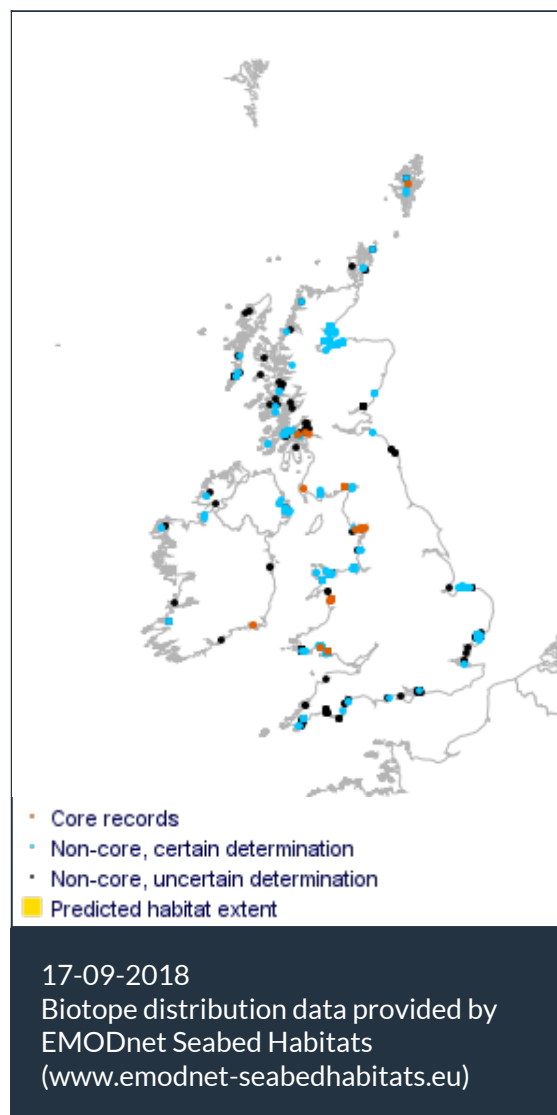


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Cerastoderma edule and polychaetes in littoral muddy sand
 Photographer: Mark Davies
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Researched by Dr Heidi Tillin & Dr Harvey Tyler-Walters

Refereed by Admin

Summary

☰ UK and Ireland classification

EUNIS 2008	A2.242	<i>Cerastoderma edule</i> and polychaetes in littoral muddy sand
JNCC 2015	LS.LSa.MuSa.CerPo	<i>Cerastoderma edule</i> and polychaetes in littoral muddy sand
JNCC 2004	LS.LSa.MuSa.CerPo	<i>Cerastoderma edule</i> and polychaetes in littoral muddy sand
1997 Biotope	LS.LMS.MS.PCer	Polychaetes and <i>Cerastoderma edule</i> in fine sand and muddy sand shores

🔍 Description

Extensive clean fine sand or muddy sand shores with abundant cockles *Cerastoderma edule*. The community consists of the polychaetes *Eteone longa*, *Scoloplos armiger*, *Pygospio elegans*, *Spio filicornis* and *Capitella capitata*, the crustaceans *Bathyporeia sarsi*, *Bodotria arenosa* and *Crangon crangon*, the spire shell *Hydrobia ulvae*, as well as the cockle *Cerastoderma edule* and the baltic tellin *Limecola balthica*. This biotope carries commercially viable stocks

of *Cerastoderma edule*, and it is therefore possible to find areas of this habitat where the infauna may have been changed through recent cockle dredging. Cockle dredging can result in a reduced bivalve abundance and reduced densities of some polychaete species, including *Pygospio elegans*. At the outer edges of large flats, there may be a zone between the cockle beds and more exposed sands, where there are fewer cockles and *Bathyporeia sarsi* is the commoner species.

The community is found mainly on the mid and lower shore where the sediment is water-saturated most of the time. Where it occurs in muddy sand, CerPo has broad transition areas with LimAre and the MEST communities, and where it occurs on clean sand shores, it may have broad transition areas with Myt.Sa. Higher on the shore, adjacent to this biotope, BatCare is found, with fewer polychaete and bivalve species due to the drier sediment found on the upper shore. A layer of mud with dense spionid polychaetes may build up on cockle beds in sheltered areas, creating a cohesive muddy layer 10-15 cm thick overlying the whole area. This may break up leaving a series of pits and patches with miniature cliffs, giving it an appearance similar to a stony shore when seen from a distance. It should be noted that where it occurs, *Peringia ulvae* tends to move a lot and may be highly variable in abundance. (Information from Connor *et al.*, 2004; JNCC 2015).

↓ Depth range

Mid shore, Lower shore

Additional information

-

✓ Listed By

- none -

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Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

The biotope description and characterizing species are sourced from Connor *et al.* (2004). This biotope is found on clean fine sand or muddy sand shores and is characterized by abundant cockles *Cerastoderma edule*. The loss of this species is likely to result in reclassification of the biotope. The presence of high densities of adult cockles may exclude other species through competition for space, sediment destabilization and modification and consumption of larvae, conversely, their removal may result in increased abundances of the associated species (Cesar, 2012). The associated species are therefore more likely to be inhibited by the presence of cockles and to benefit from their removal and the sensitivity assessments, therefore, focus on *Cerastoderma edule* as a key characterizing and structuring species.

Polychaetes associated with the biotope include *Eteone longa*, *Scoloplos armiger*, *Pygospio elegans*, *Spio filicornis* and *Capitella capitata*. The sensitivity of these species is considered generally within the biotope as this group is referred to in the title and is considered to be an important element defining the biotope, the Baltic tellin *Limecola balthica* is also present and considered within assessments.

The mud snail *Hydrobia ulvae* may migrate in and out of the biotope (Connor *et al.*, 2004) and is therefore not considered to characterize the biotope and is not considered in assessments. The crustaceans *Bathyporeia sarsi*, *Bodotria arenosa* and *Crangon crangon* may also be transient and are not specifically assessed.

Connor *et al.* (2004) note that this biotope carries commercially viable stocks of *Cerastoderma edule*, and it is, therefore, possible to find areas of this habitat where the infauna may have been changed through recent cockle dredging (see removal of target species and penetration and abrasion pressures).

The sediment habitat (fine sand or muddy sand) is a key element of the biotope, therefore, the sensitivity of this component is discussed where it is likely to be altered by the assessed pressure.

Resilience and recovery rates of habitat

Areas of dense cockles support recreational and commercial fisheries and are an important food source for some shore birds. There has, therefore, been considerable interest in the population dynamics of *Cerastoderma edule* and the effects of harvesting and this species is well-studied compared with many other soft-sediment species. In general, cockle beds undergo natural variations in density between years with periods of population stability and high densities interspersed with periods of mass mortality or more gradual decline and recovery (Ducrotoy *et al.*, 1991). The duration of the cycle of decline and recovery varies between 1 and 10 years (Ducrotoy *et al.*, 1991).

Cerastoderma edule reaches sexual maturity between 1 and 2 years may live for as long as 13 years (although most individuals live for 3-4 years). Cockles spawn annually, generally in Spring in the UK (Boyden, 1971) and fertilization is external. Males may release about 15 million sperm per second while females release about 1900 eggs per second. Gamete viability is short and fertilization is reduced 50% in 2 hrs; no fertilization occurs after 4-8 hrs. André and Lindegarh (1995) noted that fertilization efficiency was dependent on sperm concentration so that at high water flow rates

fertilisation was only likely between close individuals. However, this may be compensated for by high population densities and synchronous spawning of a large proportion of the population. The planktotrophic larvae can live in the water column for up to 5 weeks (Jonsson *et al.* 1991). The larvae, therefore, have the potential for long-distance (10s-100s of km) transport (Coscia *et al.*, 2013), supporting recruitment where local populations are removed. However, the degree of connectivity will depend on hydrodynamics (Coscia *et al.*, 2013). Following settlement, the larvae of *Cerastoderma edule* and *Limecola balthica* can disperse again through 'byssal-pelagic' dispersal (drifting on byssal threads), (de Montaudouin, 1997; Bouma *et al.* 2001; Huxham & Richards, 2003; Hiddink & Wolff, 2002; Beukema & de Vlas, 1989).

Coffen-Smout and Rees (1999) reported that cockles that had been displaced from the sediment and had not reburied could be distributed by flood and ebb tides, but especially flood tides (by rolling around the surface). *Cerastoderma edule* adults were observed to colonize cleared plots (7.65 m²) at a mean rate of 2.2 individuals/m²/14 days. Flach (1996) About 7% of a cockle population move each week (Flach, 1996; Schuitema, 1970), furrows caused by crawling cockles in aquaria during immersion were up to 50 cm in length (Richardson *et al.* 1993, although on intertidal flats smaller movements of a few centimetres were observed (Flach, 1996; Schuitema, 1970). Exposed cockles on the surface may be moved much greater distances by tidal flows (Coffen-Smout & Rees, 1999). It seems likely that small depopulated patches within dense beds could rapidly recover through adult migration. Other species associated with this biotope such as the small snail *Hydrobia ulvae*, the shrimp and amphipods and active polychaetes (including *Eteone longa* and *Scoloplos armiger*) may actively migrate into disturbed patches although more sedentary species such as the tube-dwelling *Pygospio elegans* may depend on larval recolonization rather than active migration.

No evidence was found that *Cerastoderma edule* or *Limecola balthica* can repair significant damage and it is likely that damaged individuals will suffer predation from birds, crabs, whelks and other species. However some species within the biotope can regenerate following extensive injury, *Hydrobia ulvae* have high powers of regeneration to the extent that head structures can be re-grown suggesting that individuals can recover from damage (Gorbushin *et al.*, 2001). Recovery from superficial damage may be rapid. Like other polychaetes and molluscs *Pygospio elegans* may suffer from predation by fish and birds on exposed parts of the body and can rapidly repair this (repair takes between 9-12 days (Lindsay *et al.* 2007).

Recruitment to suitable habitats and recovery of the biotope following large scale depopulation of *Cerastoderma edule* depends on episodes of good recruitment where suitable habitats remain. In the Wash, long-term time studies suggest that over the last 100 years spat fall of cockle is adequate or good in half of the years studied ; with the most recent decade studied (1990-1999) no different from previous years. This pattern of episodic recruitment is observed throughout Europe (Beukema *et al.*, 1993; Beukema & Dekker, 2005). A number of factors have been identified that affect larval supply and recruitment to the adult population. Survival during the first few months of life appears to be the decisive factor for recruitment success (Beukema & Dekker, 2005). Post-settlement mortalities are high and result from intra- and inter-specific competition and predation by shore crabs and other species (Strasser & Gunther 2001; Sanchez-Salazar *et al.* 1987a; Montaudouin & Bachelet, 1996; André *et al.* 1993; Guillou & Tartu, 1994). High densities of adult *Cerastoderma edule* and other suspension feeders may reduce settlement by ingestion of settling larvae and juveniles or smothering by sediment displaced in burrowing and feeding (Montaudouin & Bachelet, 1996). André *et al.* (1993) observed that adults inhaled 75% of larvae at 380 adults/m², and that the larvae were also ingested. However, Montaudouin and Bachelet (1996) noted that adults that inhaled juveniles rejected them and closed their siphons but

that rejected juveniles usually died. High levels of juvenile recruitment have been observed where previous severe winters with heavy storm surges have reduced the population density of adults and reduced numbers of infaunal predators (Ducrotoy *et al.*, 1991). The influence of the density of adult *Limecola balthica* (as *Macoma balthica*) on the growth and density of juveniles (1 to 5 weeks) was investigated in the field in southern Sweden (Olafsson, 1989). The results indicated that the growth of juveniles was reduced in the presence of adults at normal field density in a sublittoral, sheltered, muddy-sand sediment but was not reduced under similar conditions in a sublittoral, wave-exposed, sand sediment. The density of juveniles was not affected by adults in either habitat or in the laboratory. The growth reduction observed in juveniles at normal adult clam densities in the muddy sand habitat (where adults and juveniles are deposit feeders) but not in the sand habitat (where adults are suspension feeders and juveniles deposit feeders) indicated that intraspecific competition between adults and juveniles increases with increasing levels of dietary resource overlap between them. In areas of the Wadden Sea with a high biomass of the shrimp *Crangon crangon*, (a predator of bivalve post-larvae) annual recruitment of *Cerastoderma edule* and *Limecola balthica* (as *Macoma balthica*) was negatively related to shrimp biomass at the time of settlement (Beukema & Dekker, 2005). Bivalve recruitment appears to be enhanced following severe winters that reduce populations of predators such as the shore crab *Carcinus maenas*.

Resilience of associated species

The life history characteristics of *Limecola balthica* give the species strong powers of recoverability. Adults spawn at least once a year and are highly fecund (Caddy, 1967). Females are capable of producing 10,000-30,000 eggs (MES Ltd, 2010). There is a planktotrophic larval phase which lasts up to 2 months (Fish & Fish, 1996) and so dispersal over long distances is potentially possible given a suitable hydrographic regime. Following settlement, development is rapid and sexual maturity is attained within 2 years (Gilbert, 1978; Harvey & Vincent, 1989). In addition to larval dispersal, dispersal of juveniles and adults occurs via burrowing (Bonsdorff, 1984; Guenther, 1991), floating (Sörlin, 1988) and probably via bedload transport (Emerson & Grant, 1991). It is expected therefore that recruitment can occur from both local and distant populations.

The polychaetes *Capitella capitata* and *Pygospio elegans* have many characteristics that allow rapid colonization and population increase in disturbed and defaunated patches where there is little competition from other species (Grassle & Grassle 1974; McCall 1977). *Capitella capitata* and *Pygospio elegans* exhibit a number of reproductive strategies (a trait known as poecilogony). Larvae may develop directly allowing rapid population increase in suitable patches or they may have a planktonic stage (allowing colonization of new habitats). Experimental studies using defaunated sediments have shown that on small scales *Capitella* can recolonize to background densities within 12 days (Grassle & Grassle 1974; McCall 1977). *Capitella capitata* had almost trebled in abundance within 56 days following disturbance from tractor dredging in a clean sandy area (Ferns *et al.*, 2000). Experimental defaunation studies have shown an increase in *Pygospio elegans*, higher than background abundances within 2 months, reaching maximum abundance within 100 days (Colen *et al.* 2008). Following a period of anoxia in the Bay of Somme (north France) that removed cockles, *Pygospio elegans* increased rapidly but then decreased as cockle abundance recovered and sediments were disturbed by cockle movement (Desprez *et al.*, 1992; Rybarczyk *et al.*, 1996). Recovery will depend on the lack of stronger competitors and the supply of larvae and hence the season of disturbance will moderate recovery time. In general recovery is predicted to occur within 6 months. However, where conditions are stable these species are likely to be replaced by competitive dominants, particularly bivalves such as cockles, *Limecola balthica* or *Tellina tenuis*.

The polychaete *Eteone longa* is also considered to have some characteristics of an opportunistic

species. *Eteone longa* is a good swimmer, of high fecundity, fast growing and with pelagic larvae without sediment preferences on settlement (Rasmussen 1973; Olivier *et al.* 1992). The lifespan for this small species is probably relatively short and the growth rate fast, so this genus has the capacity to recolonize and grow to adult size in a relatively short period of time (MES Ltd, 2010). The combination of these characteristics makes it a rapid colonizer of disturbed sediments, as observed in the Tyne estuary (Hall, 1995) and at a sewage sludge disposal site off the mouth of the Tyne (Khan 1991, cited from Herrando-Perez & Frid, 2001). In the access lanes associated with oyster culture on trestles De Grave *et al.* (1998) found higher abundances of *Eteone longa* compared with undisturbed sediments. These areas may have been subject to vehicle access and the results provide additional support for the evidence from the other studies of recolonization that *Eteone longa* is an opportunistic species that preferentially colonizes disturbed areas (Rees, 1978, quoted in Hiscock *et al.*, 2002).

The polychaete *Scoloplos armiger* is also a fast growing species, breeding for the first time in its second year and living for about four years (MES Ltd, 2010), Kruse and Reise (2003) showed that populations of *Scoloplos armiger* in the intertidal with benthic development are reproductively isolated from subtidal ones with pelagic larvae. *Scoloplos armiger* hatch from egg cocoons and directly enter the sediment below the surface (Gibbs, 1968). Breeding occurs in early spring and is synchronized with spring tides. There also exist reports of a second breeding period. Although intertidal populations have a low dispersal potential (MES Ltd, 2010), benthic development supports repopulation of disturbed areas where some adults remain.

Recovery examples

In Angle Bay, Milford Haven, the presence of juvenile *Cerastoderma edule* on the lower shore shortly after the *Sea Empress* oil spill enabled the re-establishment of adult populations on the middle shore within about six months (Rostron, 1998).

Beukema *et al.* (1999) studied the recovery of the macrozoobenthic community on tidal flats (in 11 defaunated squares of about 120m² each) in the Wadden sea over 4.5 years following disturbance by anoxia. In contrast to species richness and the total number of animals, which reached values similar to those in surrounding areas as soon as the recovery period had included at least one summer, the recovery of biomass and size and age structure of long-lived species needed several years. Most species settled primarily as early postlarvae in summer while some species, including *Limecola balthica*, also settled in high numbers as juveniles in winter. The extraordinarily successful settlement of larvae of some species (including the long-lived *Limecola balthica*) in the sparsely populated plots sometimes led to substantially higher densities of these species inside the experimental plot compared to areas outside (referred to as an 'abundance overshoot'). This led the authors to conclude that inhibition of settlement outside of the experimental plots rather than facilitation within the plots was an important cause of these abundance overshoots.

Bonsdorff (1984) studied the recovery of a *Limecola balthica* (as *Macoma balthica*) population in a shallow, brackish bay in SW Finland following the removal of the substratum by dredging in the summer of 1976. Recolonization of the dredged area by *Limecola balthica* began immediately after the disturbance to the sediment and by November 1976, the *Limecola balthica* population had recovered to 51 individuals/m². One year later there was no detectable difference in the *Limecola balthica* population between the recently dredged area and a reference area elsewhere in the bay. In 1976, two generations could be detected in the newly established population indicating that active immigration of adults was occurring in parallel to larval settlement. In 1977, up to six generations were identified, giving further evidence of active immigration to the dredged area.

Ferns *et al.* (2000) found that tractor-towed cockle harvesting removed 83% of *Pygospio elegans* (initial density 1850 per m²). In muddy sand habitats, *Pygospio elegans* had not recovered their original abundance after 174 days (Ferns *et al.*, 2000). These results are supported by work by Moore (1991) who also found that cockle dredging can result in reduced densities of some polychaete species, including *Pygospio elegans*. Rostron (1995, cited in Gubbay, 1999) undertook experimental dredging of sandflats with a mechanical cockle dredger, including a site comprised of stable, poorly sorted fine sands with small pools and *Arenicola marina* casts with some algal growths. At this site, post-dredging, there was a decreased number of *Pygospio elegans* with no recovery to pre-dredging numbers after six months.

Resilience assessment. Unlike beds of other reef-forming bivalves such as the blue mussel, *Mytilus edulis* and the horse mussel *Modiolus modiolus*, which are more stable and long-lived, patches of cockles are naturally more variable over space and time (Smaal *et al.*, 2005) and beds are subject to either gradual declines as the population aged but inhibits recruitment or occasional mass mortalities that have been attributed to a number of causes (Burdon *et al.*, 2014). In habitats where this biotope occurs, there may be dense beds of cockles with adjacent patches of sediment where the cockles have been removed (by natural decline and disturbance or fisheries). These patches may be characterized by higher abundances of the opportunistic polychaetes *Capitella capitella* and *Pygospio elegans*. Small disturbed patches may be rapidly infilled by movement of adult cockles by tidal currents and wave action or active migration of adults. Active burrowing polychaetes such as *Eteone longa*, *Scoloplos armiger* and small amphipods shrimp and mud snails, *Hydrobia ulvae* may move in and out of areas of habitat.

When resistance to an impact is assessed as 'High' resilience is, therefore, assessed as 'High' by default. When resistance is assessed as 'Medium' (25% of population or habitat removed or severely impacted), resilience is assessed as 'High' based on migration and recovery from adjacent sediments (where the habitat remains suitable). As recruitment in *Cerastoderma edule* is episodic, resilience is assessed as 'Medium' (2-10 years) when resistance is 'Low' (loss of 25-75% of populations and/or habitat) or None (>75% of population removed or habitat impacted). It should be noted that small patches of disturbance within dense beds of cockles may recover rapidly through migration and displacement of cockles.

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



Hydrological Pressures

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

This biotope occurs intertidally and is, therefore, likely to be relatively tolerant of rapid changes in temperature as experienced during cyclical periods of immersion and emersion. Examples of distribution and thermal tolerances tested in laboratory experiments are provided as evidence to support the sensitivity assessment. In general, populations can acclimate to prevailing conditions which can alter tolerance thresholds and care should, therefore, be used when interpreting reported tolerances.

The key characterizing species *Cerastoderma edule* is found from Norway to Mauritania (Honkoop *et al.*, 2008) and through the Baltic, Mediterranean and Black Sea (Longshaw & Malham, 2013). The eastern border of distribution is the Murmansk coast of the Barents sea (Genelt-Yanovskiy *et al.*, 2010). The species is, therefore, likely to be exposed to warmer and colder water and air temperatures than experienced in the UK over its geographic range.

Kristensen (1958) reported that *Cerastoderma edule* from the Dutch Wadden Sea have an upper temperature tolerance of 31°C for 24 hrs, but that spat (3-6 mm) were more tolerant. All cockles died after 6 min at 36°C. Ansell *et al.* (1981) reported an upper median lethal temperature of 35°C after 24hrs (29°C after 96 hrs exposure), and Wilson (1981) reported an upper lethal temperature of 42.5°C. These temperatures are likely to exceed the pressure benchmark.

Wilson (1981) noted that *Cerastoderma edule* had limited ability to acclimate and Smaal *et al.* (1997) stated that *Cerastoderma edule* is unable to acclimate to low temperatures. However, Newell & Bayne (1980) stated that *Cerastoderma edule* was able to acclimate to a temperature change of 10°C and regulate its metabolic rate in response to rising spring temperatures. Temperature tolerance in the above studies was dependant on the environmental temperature, i.e. specimens collected in summer or areas of higher average temperature tolerated higher temperatures than specimens collected in winter and/or at lower average temperatures.

Kingston (1974) reared artificially fertilized *Cerastoderma edule* (as *Cardium edule*) in the laboratory in the temperature range 10-20°C (fertilization did not occur at 5°C). Larval growth was 'poor' at 10°C, optimal between 15 and 20°C and most larvae grew poorly and died before metamorphosing at 30°C. No larval growth occurred at 35 °C and all larvae held at this temperature were dead within 4 days of the start of the experiment. Honkoop and Van Der Meer (1998) found that winter temperatures influenced egg production by *Cerastoderma edule*, individuals kept in warmer waters produced smaller eggs.

Wilson (1993) concluded that *Cerastoderma edule* was probably tolerant of a long-term temperature rise of 2°C associated with climate change. Warmer temperatures during winter result in increased metabolic rate and hence depletion of energy reserves in a time of low food availability and may contribute to post winter mortality of adult cockles (Wilson & Elkaim, 1991). Therefore, the tolerance of *Cerastoderma edule* to temperature change will be dependent on season, an acute, short-term temperature rise in summer or decrease in winter may be detrimental.

Rapid increases in temperature during the spawning season may initiate spawning (Ducrottoy *et al.* 1991). High shore populations are likely to be more vulnerable to extremes of temperatures due to their longer emergence time (see emergence). However, Wilson (1981) showed that *Cerastoderma edule* had the highest upper lethal temperature of the species he studied, presumably due to acclimation from its close contact with the sediment surface. The upper lethal temperature of 42.8°C is unlikely to occur on mudflats except in extremely hot summers.

Changes in temperature may lead to indirect ecological consequences. Experiments demonstrated that predation on *Cerastoderma edule* by shore crabs (*Carcinus maenas*) increases as temperature increases (Sanchez-Salazar *et al.*, 1987a). Experiments were run at 6.0, 9.5, and 15.5 °C, representing the annual range of sea surface temperatures within the Menai Strait (north Wales). (Sanchez-Salazar *et al.*, 1987a). Mild winters that enhance predator survival are likely to result in increased predation of spat the following spring (Bukema & Dekker, 2005).

Other species associated with the biotope may be more tolerant of increased temperatures than *Cerastoderma edule*. The geographic range of *Limecola balthica* suggests that the species is tolerant of a range of temperatures and probably becomes locally adapted. In Europe, the species occurs as far south as the Iberian Peninsula and hence would be expected to tolerate higher temperatures than experienced in Britain and Ireland. Oertzen (1969) recorded that *Limecola balthica* (as *Macoma balthica*) could tolerate temperatures up to 49°C before thermal numbing of gill cilia occurred presumably resulting in death. Ratcliffe *et al.* (1981) reported that *Limecola balthica* from the Humber Estuary, UK, tolerated 6 hours of exposure to temperatures up to 37.5°C with no mortality. It seems likely therefore that the species could adapt to a chronic change and tolerate a large acute change with no mortality.

Field observations and laboratory experiments showed that *Limecola balthica* spawns (criterion: 50% spent) in spring when the gradual increase of the mean (monthly averaged) water temperature surpasses 8.3°C. The success of spawning and recruitment is affected by the timing of the spring phytoplankton bloom and avoidance of the main settlement of the predator *Crangon crangon* on intertidal shores (Philippart *et al.*, 2003). A mismatch in spawning cues due to an acute increase in temperature could result in low recruitment or recruitment failures.

Capitella capitata are a dominant species in mud sediments receiving effluents that are typically 8-12°C warmer than the receiving waters (Bamber & Spencer, 1984) and are considered to be tolerant to this pressure at the benchmark. *Eteone longa* and *Pygospio elegans* are summer visitors to the same effluent exposed habitats and these three species are considered tolerant of acute and chronic increases in temperature.

Sensitivity assessment. Typical surface water temperatures around the UK coast vary, seasonally from 4-19°C (Huthnance, 2010). The associated species are considered likely to be tolerant of acute and chronic increases in temperature at the pressure benchmark. *Cerastoderma edule* has a wide geographic range and as experiments suggest that individuals can survive sudden increases in temperature. As an intertidal species, with some populations occurring above mid-shore, *Cerastoderma edule* experiences rapid fluctuations in temperature over the tidal cycle. The lack of evidence for mass mortalities in very hot summers (compared with reports for low winter temperatures suggest that this species is likely to tolerate a chronic increase at the pressure benchmark (2°C for one year). An acute increase in temperature for one month may lead to changes in reproductive success and predation, particularly on spat and juveniles. Adults may, however survive. Biotope resistance is therefore assessed as 'High' and residence is 'High' (by default), the biotope is therefore considered to be 'Not sensitive'.

Temperature decrease (local)

Low

Q: High A: Low C: Medium

Medium

Q: High A: Low C: High

Medium

Q: High A: Low C: Medium

This biotope occurs intertidally and is, therefore, likely to be relatively tolerant of rapid changes in

temperature as experienced during cyclical periods of immersion and emersion. Examples of distribution and thermal tolerances tested in laboratory experiments are provided as evidence to support the sensitivity assessment. In general, populations can acclimate to prevailing conditions which can alter tolerance thresholds and care should, therefore, be used when interpreting reported tolerances.

The key characterizing species *Cerastoderma edule* is found from Norway to Mauritania (Honkoop *et al.*, 2008) and through the Baltic, Mediterranean and Black Sea (Longshaw & Malham, 2013). The eastern border of distribution is the Murmansk coast of the Barents sea (Genelt-Yanovskiy *et al.*, 2010). Populations at the Barents sea may experience annual water temperatures from 3-8°C but are exposed to air temperatures of -30°C. These populations are present between mid to low shore and although acclimated to lower temperatures are present in low densities compared to more central parts of the range (Genelt-Yanovskiy *et al.*, 2010). The low densities may be due to thermal tolerances or restrictions on feeding and growth or other factors.

High mortalities of cockle populations due to severe winters have been reported by many authors (Kristensen, 1958; Hancock & Urquhart, 1964; Beukema, 1979, 1985, 1990; Ducrottoy *et al.*, 1991; Strasser *et al.*, 2001). Kristensen (1957) showed a direct influence of temperatures below about -2°C on cockle survival (cited from Beukema, 1979). Kristensen (1958) reported that the sediment froze to a depth of 10 cm and 15 cm, resulting in death of cockles in areas of the Wadden Sea in the severe winter of 1954. Hancock & Urquhart (1964) report almost 100% mortality of cockles in Llanrhidian Sands, Burry Inlet and high mortalities of cockles in other areas around the UK after the winter of 1962/63. However, enhanced recruitment of bivalves, including *Cerastoderma edule* and *Limecola balthica* has been observed in European estuaries after colder winters while densities following milder winters are lower (Beukema 1991; Walker & Dare, 1993; Young *et al.*, 1996). The factors indirectly responsible for this pattern may be changes in reproductive success (Honkoop & Van Der Meer, 1998), changes in the spring phytoplankton bloom, predation (Beukema & Dekker, 2005), removal of larvae by off-shore currents and removal of adults (enhancing recruitment via reduced ingestion of larvae (André *et al.*, 1993) and reduced competition between adults and juveniles).

The geographical distribution of *Limecola balthica* suggests that it is very tolerant of low temperature. The species occurs in the Gulfs of Finland and Bothnia where the sea freezes for several months of the year (Green, 1968). It must, therefore, tolerate much lower temperatures than it experiences in Britain and Ireland. Furthermore, *Limecola balthica* was apparently unaffected by the severe winter of 1962/3 which decimated populations of many other bivalve species (Crisp, 1964), and De Wilde (1975) noted that *Limecola balthica* kept at 0°C maintained a high level of feeding activity. It is unlikely, therefore, that UK populations of *Limecola balthica* would be intolerant of decreases in temperature.

Sensitivity assessment. Typical surface water temperatures around the UK coast vary, seasonally from 4-19°C (Huthnance, 2010). The biotope is considered to tolerate a chronic change at the pressure benchmark (2°C decrease in temperature for a year). An acute reduction in temperature may be tolerated by adults and spat outside of winter (although acclimation to warmer temperatures means that impacts on spawning and growth may occur). An acute reduction in temperature during winter may exceed thermal tolerances, biotope resistance (based on *Cerastoderma edule*) is therefore assessed as 'Low' and resistance is assessed as 'Medium'. Biotope sensitivity is therefore judged to be 'Medium', this precautionary assessment is presented in the table.

Salinity increase (local)**Low**

Q: High A: Medium C: Medium

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Medium C: Medium

This biotope is reported to occur in full (30-35 ppt) reduced (18-30 ppt) and variable (18-35 ppt) salinity (JNCC, 2015). A change at the pressure benchmark is considered to represent an increase to >40 ppt (the biotope is considered 'Not sensitive to an increase in salinity from variable or reduced to full). Little evidence was found for tolerances of elevated salinity although populations are likely to be acclimated to short-term increased salinities in surface sediment layers as evaporation on hot days, or wind driven desiccation leads to increased salinities.

Boyden & Russell (1972) stated that *Cerastoderma edule* prefers salinities between 15 and 35 psu. Russell & Peterson (1973) reported lower median salinity limits of 12.5 psu and upper median salinity limits of 38.5 psu. Rygg (1970) noted that *Cerastoderma edule* did not survive 23 days exposure to <10 psu or at 60 psu, although they did survive at 46 psu. Rygg (1970) also demonstrated that salinity tolerance was temperature dependent (after 3 days, 100% survival at 33 psu and 35-38°C, but 50% mortality occurred at 20 psu and 37°C and 100% mortality at 13 psu and 37°C). Wilson (1984) noted that *Cerastoderma edule* remained open during 1 hour exposure to salinities between 13.3 and 59.3 psu. It should be noted that the tolerances reported above depend on the duration of the experiment.

Kingston (1974) found that *Cerastoderma edule* larvae grew optimally at 30 and 35 psu, and grew well at 40 psu but the growth increment declined at 45 psu and larvae did not metamorphose. He noted that *Cerastoderma edule* larvae survived between 20 -50 psu, but died after 11 days at 55 psu or 10 days at 10 psu.

The associated species *Limecola balthica* is found in brackish and fully saline waters (although it is more common in brackish waters) (Clay, 1967). McLusky & Allan (1976) conducted salinity survival experiments on *Limecola balthica* (as *Macoma balthica*) over a period of 150 days. No deaths were reported in specimens of *Limecola balthica* maintained at 30.5 psu for the duration of the experiment but *Limecola balthica* failed to grow at 41 psu.

Sensitivity assessment. Little evidence was found to assess this pressure at the benchmark. Although species within the biotope are likely to tolerate short-term increases in salinity in sediment surface layers between tidal cycles a longer change is likely to exceed salinity tolerances of adults and larvae. Biotope resistance is assessed as 'Low' as the results of Rygg (1970) suggest some adults may survive and acclimate. Biotope resilience (following a return to suitable habitat conditions) is assessed as 'Medium' and sensitivity is assessed as 'Medium'.

Salinity decrease (local)**Medium**

Q: High A: Medium C: High

High

Q: High A: Low C: Medium

Low

Q: High A: Low C: Medium

This biotope is reported to occur in full (30-35 ppt) reduced (18-30 ppt) and variable (18-35 ppt) salinity (JNCC, 2015). As the characterizing species are found in biotopes in both full and variable salinity habitats, the biotope is considered 'Not sensitive' to a decrease in salinity from full to reduced or variable. The pressure benchmark is assessed as a change to 'Low' salinity (<18 ppt). *Cerastoderma edule* and associated species within this biotope are exposed to periods of potential hypo-saline conditions resulting from heavy rainfall and freshwater runoff. The available studies indicate that *Cerastoderma edule* larvae and adults show a wide tolerance range of salinity for both adults and larvae, in accordance with the intertidal distribution. Kristensen (1958), however,

reported the death of young spat (1-2 mm) in the Dutch Wadden Sea due to heavy rain, whereas the adults were able to dig deeper into the sediment, reducing exposure.

Boyden & Russell (1972) stated that *Cerastoderma edule* prefers salinities between 15 and 35 psu. Russell & Peterson (1973) reported lower median salinity limits of 12.5 psu and upper median salinity limits of 38.5 psu. Rygg (1970) noted that *Cerastoderma edule* did not survive 23 days exposure to <10 psu. Rygg (1970) also demonstrated that salinity tolerance was temperature dependant (after 3 days, 100% survival at 33 psu and 35-38°C, but 50% mortality occurred at 20 psu and 37°C and 100% mortality at 13 psu and 37°C). Wilson (1984) noted that *Cerastoderma edule* remained open during 1 hour exposure to salinities between 13.3 and 59.3 psu. It should be noted that the tolerances reported above depend on the duration of the experiment.

Russell (1969) found that the optimum salinity for the survival of an adult cockle varies with the mean environmental salinity and suggested that the different salinity tolerance, demonstrated for various populations of *Cerastoderma edule* are not inherent interspecific differences, but a result of localized environmental acclimation. It is possible that larvae settling in regions of low salinity could have developed elsewhere, under more favourable conditions, and have become gradually acclimatized to the low salinity conditions; alternatively, the larvae produced by parents from a low salinity environment might be adapted to lower salinities than those produced by populations from higher salinity (Russell, 1969).

McLusky & Allan (1976) conducted salinity survival experiments with *Limecola balthica* (as *Macoma balthica*) over a period of 150 days. Survival times declined with decreased salinity. At 12 psu, specimens survived 78 days, whilst specimens at 8.5 psu survived 40 days. Some specimens of *Limecola balthica* survived 2.5 days at 0.8 psu, which was apparently due to the animals ability to clamp its valves shut in adverse conditions. McLusky & Allan (1976) also reported that *Limecola balthica* failed to grow (increase shell length) at 15 psu. *Limecola balthica* is found in brackish and fully saline waters (Clay, 1967) so may tolerate a state of flux. Its distribution in combination with the experimental evidence of McLusky & Allan (1976) suggests that *Limecola balthica* is likely to be very tolerant to a decreased salinity over a short period. A decline in salinity in the long-term may have implications for the species viability in terms of growth, and the distribution of the species may alter as specimens at the extremes retreat to more favourable conditions.

Sensitivity assessment. The available evidence suggests that adult *Cerastoderma edule* may survive a reduction in salinity to just below 18 ppt and populations may become locally acclimated to reduced salinities. As a reduction may lead to some mortalities and a reduction in growth and reproductive success of the key characterizing *Cerastoderma edule*, biotope resistance is assessed as 'Medium', recovery (following a return to usual habitat conditions) is assessed as 'High' and sensitivity is therefore assessed as 'Low'.

Water flow (tidal current) changes (local)

Medium

Q: High A: Low C: Low

High

Q: High A: Low C: Medium

Low

Q: High A: Low C: Low

Cockles are dependent on water flow to deliver suspended food particles. The hydrodynamic regime strongly influences the sediment structure and removal of biodeposits and faeces, oxygenation, food supply and recruitment. *Cerastoderma edule* prefers muddy-sand to sandy-mud or fine sand substrates. Increases in water flow above the critical erosion rate would re-suspend fine sediments and would alter the habitat. Increased sediment coarseness would reduce habitat suitability (as assessed below). Decreasing water flow rate in sheltered habitats may increase siltation and favour muddy substrates that are less suitable for *Cerastoderma edule*. Boyden and

Russell (1972) suggested that lack of tidal flow may exclude *Cerastoderma edule* possibly due to reduced food availability as suggested by Brock (1979). According to regression models developed by Ysebaert et al. (2002), *Cerastoderma edule* occurs in environments subject to flow velocities of up to 0.8 m/s, having a maximum predicted probability of occurrence at flow velocities around 0.35 m/s.

Newly settled spat and juveniles (<4.8 mm) are capable of bysso-pelagic dispersal., Water flow rates probably affect the distribution and dispersal of juveniles. Increasing water flow may remove adult cockles from the sediment surface and carry them to unfavourable substratum or deep water, where they may be lost from the population. Coffen-Smout and Rees (1999) reported that exposed cockles on the sediment surface could be distributed up to 0.45 m on neap tides or between 94 m and 164 m on spring tides. Theoretical estimates suggest that the critical force for displacing exposed cockles is 0.3 m/s (Coffen-Smout & Rees, 1999).

Experimental studies of water velocity and clearance rate in *Cerastoderma edule* have produced a range of results which may be due to genetic or phenotypic differences in test populations (Widdows & Navarro, 2007). Wildish & Miyares (1990) recorded a reduction in flume experiments found that feeding efficiency was greatest at 0.15 m/s and gradually declined to 0.45 m/s, there was no significant difference in feeding rate between current velocities of 0.05 and 0.35 m/s (Widdows & Navarro, 2007). At 0.45 m/s, sand grains (1-3 mm) began to roll along the bed and this may have reduced clearance rate. At 0.7 m/s, feeding appeared to cease due to the movement of sediment as well as cockles (Widdows & Navarro, 2007).

Sensitivity assessment. The associated burrowing species are considered to be 'Not Sensitive' to this pressure, as burrowing life habits coupled with deposit or predatory feeding types were considered to be protective. Many of these species are also found on mudflats and hence have little to no sensitivity to this pressure as species-specific habitat suitability would not decrease. The characterizing *Cerastoderma edule* were considered to have some resistance to this pressure as they are found within a range of flow speeds and can feed at a range of flow speeds. However decreased flow rates (at the pressure benchmark) in sheltered habitats may reduce food supply and enhance sediment deposition favouring deposit feeders. At the pressure benchmark some biotopes may be affected by an increase or decrease at the pressure benchmark through effects on sediment and delivery of suspended food, biotope resistance is assessed as 'Medium' and resilience is assessed as 'High' as the changes may be outweighed by seasonal events such as storms. Therefore, sensitivity is assessed as 'Low'.

Emergence regime changes

Low

Q: High A: High C: Medium

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Cockle dominated biotopes can range from mean high water springs (Sanchez-Salazar *et al.*, 1987b) to the sublittoral (JNCC, 2015). Shore height influences a number of factors that affect cockle condition and survival and the size and age structure of populations can vary significantly with shore height (Sanchez-Salazar *et al.*, 1987b), hence, this biotope is likely to be sensitive to changes in emergence (both increase and decrease).

At lower shore levels predation by shore crabs and fish may structure populations by removing smaller individuals and may set the lower distribution limit while at higher shore levels predation by oystercatchers targets larger size classes (Sanchez-Salazar *et al.*, 1987b). Shore height will also influence emergence times, higher shore populations are exposed to air temperatures for longer that may be warmer and colder than seawater creating thermal shocks, higher shore individuals

will also have less time to feed, resulting in reduced growth (Jensen, 1992) body condition which may increase susceptibility to parasites and other factors (Wegeberg & Jensen, 2003). Dense populations lower on the shore may also deplete the available suspended food, reducing the supply to higher shore populations (Peterson & Black, 1987, 1991; Kamermans, 1993).

DeMontadouin and Bachelet (1996) manipulated low and high population densities (160-2000 adults/m² and tidal elevation (low and mid-water levels of *Cerastoderma edule* at Arcachon bay, SW France to test the influence of adult densities and emersion time on growth, settlement and survival. Growth rates were affected by tidal height with higher growth rates at low water levels.

Sensitivity assessment. A change in emersion is likely to alter the habitat suitability for *Cerastoderma edule* and associated species, resulting in changes in assemblage structure, biotope resistance is therefore assessed as 'Low' and resilience is assessed as 'Medium' following a return to previous habitat condition. Biotope sensitivity is therefore assessed as 'Medium'.

Wave exposure changes (local)

High

Q: High A: Low C: NR

High

Q: High A: High C: High

Not sensitive

Q: High A: Low C: Low

This biotope is recorded from locations that are judged to range from extremely sheltered to moderately exposed (JNCC, 2015). As the biotope and characterizing and associated species are found across a range of wave exposures, populations occurring within the middle of the range are considered to have 'High' resistance to a change in significant wave height at the pressure benchmark. Resilience is assessed as 'High', by default, and the biotope is considered 'Not sensitive' Changes in wave exposure greater than the pressure benchmark are likely to have marked effects on the sediment dynamics of the shore. Increased exposure could result in increased grain size or erosion of the sediment while decreased exposure will lead to increased siltation and reduced grain size (muddy sediment). In both cases, the sediment may become unsuitable for *Cerastoderma edule* populations resulting in a reduction of the extent or abundance of the population (see physical change pressures). Increased wave action during storms may also remove adult cockles from the sediment surface which may be subsequently lost from the population. These changes are not assessed in this section as they are considered to be the result of changes in wave action that exceed the pressure benchmark.

Chemical Pressures

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

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

The species present in the biotope may, however, be sensitive to increases in contaminants greater than the pressure benchmark. Studies of *Cerastoderma edule* populations from polluted and un-contaminated sites in Southampton Water showed that tissue heavy metal concentrations were lower in summer than winter/spring, tissue heavy metal concentrations decreased with size of the cockle, and that cockles in sediments contaminated with metals and hydrocarbons had lower life expectancies, growth rates and body condition index (Savari *et al.*, 1991a,b).

Bryan (1984) suggested that many polychaetes were resistant to heavy metals and evidence from the work of Bryan & Gibbs (1983) in the metal polluted Fal estuary supports this view. Bivalves, on the other hand, including *Cerastoderma edule* displayed a much lower tolerance and were found to be the most obvious absentees from the polluted Restronguet Creek area of the Fal (Bryan & Gibbs, 1983). Adult *Cerastoderma edule* were found to be more tolerant to metal toxicity than the juvenile or larval stages which appear unable to withstand the high concentrations of copper and zinc. However, transplantation of *Cerastoderma edule* into Restronguet Creek (highly polluted by heavy metals) resulted in 10-15% mortality within 63 days but 100% within about four months. The toxic body-burden of copper to *Cerastoderma edule* was found to be ca. 250 µg / g with zinc being less toxic. Bryan & Gibbs (1983) stated that *Cerastoderma edule* takes up heavy metals mainly from solution rather than from sediment and that it was excluded from Restronguet Creek by the high levels of Cu and Zn.

A 2-year microcosm experiment was undertaken to investigate the impact of Cu on the benthic fauna of the lower Tyne Estuary (UK) by Hall and Frid (1995). During a 1-year simulated contamination period, 1 mg l⁻¹ Cu was supplied at 2-weekly 30% water changes, at the end of which the sediment concentrations of Cu in contaminated microcosms reached 411 µg g⁻¹. Toxicity effects reduced populations of the four dominant taxa, including *Capitella capitata*. When Cu dosage was ceased and clean water supplied, sediment Cu concentrations fell by 50% in less than 4 days, but faunal recovery took up to 1 year, with the pattern varying between taxa. Since the Cu leach rate was so rapid it is concluded that after remediation, contaminated sediments show rapid improvements in chemical concentrations, but faunal recovery may be delayed with experiments in microcosms showing faunal recovery taking up to a year.

Rygg (1985) classified *Scoloplos armiger*, *Capitella capitata* and *Eteone longa* as highly tolerant species, common at the most Cu polluted stations (Cu >200 mg/Kg) in Norwegian fjords. Bryan & Gibbs (1983) found that *Pygospio elegans* appear to have adapted to the very high concentrations of copper and zinc in Restronguet Creek in the highly contaminated Fal estuary and the larvae are subjected to widely fluctuating conditions of salinity and relatively high metal concentrations.

In a review of chemical use on salmon aquaculture, Burridge *et al.* (2008) described how despite the binding of copper in sediments, it can be toxic (copper is used as an antifoulant and may also be a constituent of the food fed to farmed salmon). Sediments under salmon cages in the Bay of Fundy and at various distances away from the cages were evaluated for toxicity and in addition to elevated levels of copper (above the threshold effects level), the sediments also had elevated zinc, other metals, ammonia nitrogen, sulphide, total organic carbon, and other organic compounds. Sediments enriched in copper, zinc and silver caused decreased reproduction in the clam *Limecola balthica*, due to failed gamete production. Reproductive recovery occurred when contamination decreased (Hornberger *et al.*, 2000). It was noted that studies from field sites have numerous metals rather than just copper alone, and it is difficult to attribute toxicity to any particular metal.

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.

The species present in the biotope may, however, be sensitive to increases in contaminants greater than the pressure benchmark. Laboratory studies have demonstrated that *Cerastoderma edule* is sensitive to oil and polycyclic aromatic hydrocarbons (Wootton *et al.*, 2003) and the available evidence indicates that *Limecola balthica* is also sensitive to acute and chronic exposure. Some of

the polychaetes associated with this biotope are either more tolerant of hydrocarbons (*Eteone longa*) or their populations are able to recover rapidly (*Pygospio elegans* and *Capitella capitata*).

Following the Sea Empress oil spill in Milford Haven, Wales, high mortalities of the cockles *Cerastoderma edule* were reported and large numbers of moribund and dead marine animals, including *Cerastoderma edule*, were washed ashore after the Sea Empress oil spill, however, no commercial stocks were affected (Rostron, 1998; SEEC 1998). In Angle Bay, the presence of juveniles lower down the shore shortly after the spill enabled the reestablishment of adult populations on the middle shore within about six months. Additional species recorded at Sandy Haven in the summer following the spill included the polychaetes *Pygospio elegans* and *Capitella capitata*: the abundance of *Capitella capitata* increased dramatically at one site (Rostron, 1998).

McLusky (1982) examined the fauna of the intertidal mudflats at Kinneil in the Forth estuary that received petroleum, chemical and domestic effluents. Spatfall of *Cerastoderma edule* occurred in 1976 but the abundance declined steadily between 1976 and 1980. *Cerastoderma edule*, together with many other species, was excluded from sediment within 1.5 km of effluent discharges. Between 1.5-2.25 km the abundance of fauna, including *Cerastoderma edule* increased markedly (McLusky, 1983).

Stekoll *et al.* (1980) exposed the associated species, *Limecola balthica* (as *Macoma balthica*), to Prudhoe Bay crude oil in flowing seawater for six months at three concentrations; low 0.03 mg/l, medium 0.3 mg/l and high 3.0 mg/l and concluded that chronic exposure of *Limecola balthica* to oil-in-seawater concentrations even as low as 0.03 mg/l would in time lead to population decreases. The individuals in this study were not subjected to any of the stresses that normally occur in their natural environment on mudflats such as changes in salinity, temperature, oxygen availability and wave action, therefore, it is possible that exposure of *Limecola balthica* to oil under field conditions results in higher mortality.

Shaw *et al.*, (1976) also reported mortality of *Limecola balthica* (as *Macoma balthica*) caused by exposure to crude oil following an experimental application of oil at a concentration of 1.2 µl oil/cm² and 5.0 µl oil/cm² to sediments which equated to oil spills of one ton /20 km² and one ton/100 km². Significant mortalities were observed after only two days following application of the oil at a concentration of 5.0 µl oil/cm². Some specimens of *Limecola balthica* survived the application of oil in these experiments but were weakened.

Eteone longa was described by Hiscock *et al.*, (2005) (based on Levell *et al.* (1989) as a very tolerant taxon to oil pollution and were found in enhanced abundances in the transitional zone along hydrocarbon contamination gradients surrounding oil platforms.

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

Not relevant (NR)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

No evidence.

Introduction of other substances

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation

Medium

Q: High A: High C: Medium

High

Q: High A: Low C: Medium

Low

Q: High A: Low C: Medium

Muddy sands may have relatively low oxygen concentrations, lower than coarse sands but higher than muds. The effects of changes in dissolved oxygen concentration on the marine environment can be sub-divided into direct effects (those organisms directly affected by changes in dissolved oxygen concentration) and secondary effects (those arising in the ecosystem as a result of the changes in the organisms directly affected). The direct effects of changes in dissolved oxygen (DO) concentrations are primarily related to reduced DO levels and include lethal and sub-lethal responses in marine organisms, the release of nutrients, and the development of hypoxic and anoxic conditions. Anaerobic conditions in the sediments increases microbial activity and reduces the redox potential of the sediments (Fenchel & Reidl, 1970). Ultimately this increases the production of toxic chemicals such as hydrogen sulphide and methane. The changed status to anaerobiosis will limit the sediment macroinfauna to species which can form burrows or have other mechanisms to obtain oxygen from overlying water. Anoxic conditions may alter community structure and reduce diversity and abundance and interfere with bird feeding (Simpson, 1997, cited in Elliott *et al.*, 1998).

A number of animals have behavioural strategies to survive periodic events of reduced dissolved oxygen. These include avoidance by mobile species such as crustaceans, shell closure and reduced metabolic rate in bivalve molluscs and either decreased burrowing depth or emergence from burrows for sediment dwelling crustaceans, molluscs and annelids. The sensitivity to reduced oxygen and recovery from episodes of hypoxia and anoxia varies between the characterizing and associated species of this biotope. The available evidence suggests that *Cerastoderma edule* is more sensitive to this pressure than *Limecola balthica* and the polychaete species.

Rosenberg *et al.* (1991) reported 100% mortality of *Cerastoderma edule* exposed to 0.5-1.0ml/l oxygen for 43 days and 98% mortality after 32 days. *Cerastoderma edule* migrated to the surface of the sediment in response to decreased oxygen concentrations. Theede *et al.* (1969) reported 50% mortality after 4.25 days at 1.5 mg/l oxygen. Theede *et al.* (1969) also noted that *Cerastoderma edule* only survived 4 days exposure to 0.0-6.1 cm³/l of hydrogen sulphide, which is associated with anoxic conditions. This suggests that *Cerastoderma edule* could survive short periods of anoxia but it is likely that continued exposure to 2 mg/l oxygen for a week would be lethal.

Fifty percent (LT50) of cockles in anoxic seawater died after 3.5 days (Babarro & de Zwaan, 2001) The anoxic survival time of *Cerastoderma edule* from two different ecosystems and differing anoxia tolerances was studied in static (closed) and flow-through systems. The antibiotics chloramphenicol, penicillin and polymyxin were added, and molybdate (a specific inhibitor of the process of sulfate reduction). Median mortality times were 2.7 and 2.9 days for *Cerastoderma* for static and flow-through incubations, respectively. The addition of chloramphenicol increased strongly survival time in both systems with corresponding values of 6.4 and 6.5 days for *Cerastoderma*. Overall the results indicate that proliferation of anaerobic pathogenic bacteria, associated with the bivalves, is a main cause of death besides the lack of oxygen. Bacterial damage is probably caused by injury of the tissues of the clams and not by the release of noxious

compounds to the medium (de Zwaan et al. 2002).

Limecola balthica appears to be relatively tolerant of deoxygenation. Brafield & Newell (1961) frequently observed that in conditions of oxygen deficiency (e.g. less than 1 mg O₂/l) *Limecola balthica* (as *Macoma balthica*) moved upwards to fully expose itself on the surface of the sand. Specimens lay on their side with the foot and siphons retracted but with valves gaping slightly allowing the mantle edge to be brought into full contact with the more oxygenated surface water lying between sand ripples. In addition, *Limecola balthica* was observed under laboratory conditions to extend its siphons upwards out of the sand into the overlying water when water was slowly deoxygenated with a stream of nitrogen. The lower the oxygen concentration became the further the siphons extended. Dries & Theede (1974) reported the following LT50 (medial lethal time) values for *Limecola balthica* maintained in anoxic conditions: 50 - 70 days at 5°C, 30 days at 10°C, 25 days at 15°C and 11 days at 20°C. Theede (1984) reported that the ability of *Limecola balthica* to resist extreme oxygen deficiency was mainly due to cellular mechanisms. Of considerable importance are sufficient accumulations of reserve compounds e.g. glycogen and the ability to reduce energy requirements for maintenance of life by reducing overall activity (Theede, 1984). *Limecola balthica* is, therefore very tolerant of hypoxia, although it may react by reducing metabolic activity. Intolerance is, therefore assessed as low. Metabolic function should quickly return to normal when normoxic levels are resumed and so recoverability is recorded as very high. *Limecola balthica* have been shown experimentally to be able to resist time periods of 9 weeks under algal cover (arising from organic enrichment), their long siphon allowing them to reach oxygenated water (Thiel et al., 1998).

Dense *Capitella capitata* populations are frequently located in areas with greatly elevated organic content, even though eutrophic sediments are often anoxic and highly sulfidic (Tenore, 1977; Warren, 1977; Tenore & Chesney, 1985; Bridges et al., 1994). The polychaetes *Capitella capitata*, *Pygospio elegans* and *Scoloplos armiger* have all been reported to recolonize habitats following periods of anoxia and hypoxia. Following a period of anoxia in the Bay of Somme (north France) that removed cockles, *Pygospio elegans* increased rapidly but then decreased as cockle abundance recovered (Desprez et al., 1992; Rybarczyk et al., 1996).

Scoloplos armiger has been described as being present in low oxygen areas and as a dominant species in the recolonization of previously anoxic areas (Pearson & Rosenberg, 1978). Intertidal *Scoloplos armiger* is, in contrast to subtidal specimens, subject to hypoxia when tidal flats are without oxygenated seawater during low tide (Kruse et al., 2004). Tolerance against hypoxia and sulfide is low (Kruse et al., 2004), and worms may ascend into the oxic layer during low tide (Schoettler & Grieshaber, 1988).

Sensitivity assessment. Decreased oxygen levels, would lead to an alteration in sediment chemistry, including the production of hydrogen sulphides that would alter habitat conditions and is likely to lead to mortality of *Cerastoderma edule* although the characterizing species are likely to be more tolerant. Based on Theede et al., 1996, the sensitivity of the biotope (based on *Cerastoderma edule*) is 'Medium' as periodic immersion would reoxygenate sediments and exposure is likely to be short-term, limiting mortality. Resilience is assessed as 'high' and sensitivity is assessed as 'Low'.

Nutrient enrichment

High

Q: Low A: NR C: NR

High

Q: High A: High C: High

Not sensitive

Q: Low A: Low C: Low

This pressure relates to increased levels of nitrogen, phosphorus and silicon in the marine

environment compared to background concentrations. The benchmark is set at compliance with WFD criteria for good status, based on nitrogen concentration (UKTAG, 2014).

Changes in the nutrient concentrations (e.g. nitrogen and phosphates) are likely to have indirect rather than direct effects on *Cerastoderma edule*. Increased levels of nutrients at low level may increase phytoplankton productivity and increase food availability for *Cerastoderma edule*. However, higher nutrient inputs are associated with eutrophication, resulting in increased oxygen consumption and decreased oxygen concentration. Rosenberg and Loo (1988) suggested that the mass mortalities of *Cerastoderma edule* observed in Laholm Bay, western Sweden during the 1980s was correlated with increased nutrient levels, and associated decrease in oxygen levels during this period (see oxygenation below). However, no direct causal link was established.

Desprez et al. (1992) implicated a eutrophication-induced plankton bloom as the cause of the decline of *Cerastoderma edule* populations in the Bay of Somme, France. Prior to the event in 1982, densities were several 1000 / m² but by 1982, this had fallen to just a few hundred individuals / m². By 1987, the cockle population had returned.

Sensitivity assessment. As *Cerastoderma edule* and other characterizing species in the biotope are not primary producers they are not considered directly sensitive to an increase or decrease in plant nutrients in the water column. Phytoplankton and algal detritus may be utilised as food by this genus but supply is not considered to be affected at the pressure benchmark levels. This species is therefore considered to be 'Not Sensitive' to this pressure. Resistance is therefore assessed as 'High' and resilience as 'High' (by default).

Organic enrichment

High

Q: High A: Medium C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: High

Benthic responses to organic enrichment have been described by Pearson & Rosenberg (1978) and Gray (1981). Moderate enrichment increases food supply enhancing productivity and abundance. Tidal flats (especially mudflats) can be sensitive to organic enrichment which can result in blooms of opportunistic ephemeral seaweeds such as *Enteromorpha* spp. These can form dense mats, shading the mud surface and leading to anoxic conditions- altering community structure and reducing diversity and abundance and interference with bird feeding (Simpson, 1997). *Limecola balthica* have been shown experimentally to be able to resist time periods of 9 weeks under algal cover, their long siphon allowing them to reach oxygenated water although other bivalves decreased in abundance (Thiel *et al.*, 1998). Organic enrichment beneath oyster cultivation trestles and mussel cultivation sites and fish cages has led to community replacement/dominance by Cirratulid, Capitellid and Spionid polychaetes, particularly *Manayunkia aesturina* in mudflats, that characterize disturbed areas enriched in organic matter (Pearson & Rosenberg 1978, Samuelson 2001, see Bouchet and Saurier 2008 for references for activities). Hydrographic and physical conditions (water depth, currents, bottom substrate type) determine particulate matter deposition at any given location, organic matter accumulation in or on the bottom and resulting changes in oxygen status due to aquaculture, can be highly variable within a small area. Gross effects will lead to anoxic, defaunated sediments which may be covered by sulphur reducing bacteria such as *Beggiatoa* spp. (Elliott *et al.* 1998). Diatom density may be reduced by organic enrichment potentially reducing the stability of mudflats (Elliott *et al.* 1998).

Cerastoderma edule and *Pygospio elegans* have been categorised through expert judgement and literature review as AMBI Group III- species tolerant to excess organic matter enrichment. These species may occur under normal conditions, but their populations are stimulated by organic

enrichment (slight unbalance situations). They are surface deposit feeding species (Borja *et al.*, 2000, validated by Gittenberger & van Loon, 2011). Where high levels of organic enrichment occur, bacterial demand may lead to decreases in oxygen (as assessed below). *Eteone longa* has been described as tolerant of nutrient enrichment (Pearson & Rosenberg, 1978). *Scoloplos armiger*, *Eteone longa* and *Eteone flava* have been characterized as AMBI Group III. Species tolerant to excess organic matter enrichment. These species may occur under normal conditions, but their populations are stimulated by organic enrichment (slight unbalance situations). They tend to be surface deposit feeding species (Borja *et al.* 2000 and Gittenberger & van Loon 2011). However, a later review characterized *Scoloplos armiger* as Group II Species indifferent to enrichment, always present in low densities with non-significant variations with time (from the initial state, to slight unbalance). These include suspension feeders, less selective carnivores and scavengers. They tend to be surface deposit-feeding species (Gittenberger & van Loon, 2011).

Dense *Capitella capitata* populations are frequently located in areas with greatly elevated organic content, even though eutrophic sediments are often anoxic and highly sulfidic (Tenore, 1977; Warren, 1977; Tenore & Chesney, 1985; Bridges *et al.* 1994) e.g. sewage-enriched sediments in Kiel Bay (Gray, 1979).

Studies have also identified *Pygospio elegans* as a 'progressive' species, i.e. one that shows increased abundance under organic enrichment (Leppakoski, 1975, cited in Gray, 1979). In the sewage-enriched sediments of Kiel Bay, *P. elegans* is the numerical dominant.

Sensitivity assessment. Areas with significant mud contents are likely to be rich in organic matter and low oxygen penetration coupled with high levels of bacterial activity means sediments anoxic a short distance below the surface. Given their adaptation to these habitat conditions the characterizing *Cerastoderma edule* and other associated species are not considered sensitive to organic enrichment. Indeed, some species present e.g. *Capitella* and *Pygospio elegans* are typical of enriched and anoxic sediments. The biotope is considered 'Not sensitive' to this pressure based on 'High' resistance and 'High' recovery (by default).

A Physical Pressures

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

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

Physical change (to another seabed type)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High
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This biotope occurs in fine sands and muddy sands (JNCC, 2015). A change to natural or artificial hard substratum would remove this sedimentary biotope and the species. If pockets of fine sediment accumulate in pockets within the substrata then these areas may be re-colonised by species associated with this biotope but these pockets of sediment would not be equivalent to the

biotope. Recovery will depend on the re-instatement of suitable habitat.

Sensitivity assessment. Based on the loss of suitable habitat, biotope resistance to this pressure is assessed as 'None'. Resilience is assessed as 'Very low' as the pressure benchmark refers to a permanent change. Biotope sensitivity is, therefore 'High'.

Physical change (to another sediment type)

None

Q: High A: High C: High

Very Low

Q: High A: High C: High

High

Q: High A: High C: High

The benchmark for this pressure refers to a change in one Folk class. The pressure benchmark originally developed by Tillin *et al.* (2010) used the modified Folk triangle developed by Long (2006) which simplified sediment types into four categories: mud and sandy mud, sand and muddy sand, mixed sediments and coarse sediments. The change referred to is therefore a change in sediment classification rather than a change in the finer-scale original Folk categories (Folk, 1954). The change in one Folk class is considered to relate to a change in classification to adjacent categories in the modified Folk triangle (Long, 2006). As this biotope occurs within fine sands and muddy sands (JNCC, 2015), the change at the pressure benchmark refers to a potential change to coarse sediments, mixed sediments, sand and muddy sands or mud.

The particle size of sediments and correlated physical and chemical factors (such as drainage, organic matter content and hydrodynamic regime), is a key determinant of the structure of benthic invertebrate assemblages (Van Hoey *et al.*, 2004; Yates *et al.*, 1993). Free draining coarse sediments such as shingle and gravels have low levels of water and organic content and cohesion and high levels of abrasion as the particles are moved by wind or water action. Although Hall & Harding (1997) report that *Cerastoderma edule* are found in stoney gravel this is not an optimal sediment for supporting dense populations and coarse sediment shores do not support many of the associated species found in this biotope. A change to coarse sediments would result in loss of characterizing and associated species, resulting in biotope reclassification. In North America, cultivation of clam species including the Manila clam *Tapes philippinarum* usually involves some form of habitat modification in the form of adding gravel or gravel and crushed shell over mud and sand beaches, to create a more productive clam habitat (referred to as 'gravelled clam plots'). Such habitat modifications lead to alterations in the local environment and consequently faunal composition. Simenstad & Fresh (1995, cited in Kaiser & Beadman, 2002) reported that the application of gravel to intertidal sediments resulted in a shift from a polychaete to a bivalve and nemertean dominated community, but emphasised that changes are likely to be site-specific.

Infauna can be affected by changes in sediment as many are adapted to burrow through certain grades of sediment (Trueman & Ansell, 1969), decreased fine fractions will reduce habitat suitability for species that maintain permanent burrows. Changes in sedimentary features may also influence the proportions of suspension and deposit feeding animals (Sanders, 1968), with deposit feeders favoured by increases in the proportion of silts and clays.

A study in the Dutch Wadden Sea showed that suction-dredging for cockles (*Cerastoderma edule*) led to a significant long-term reduction in settlement and stocks of the target bivalve species (Piersma *et al.*, 2001). Analysis of sediment characteristics before and after dredging showed an increase in median grain size and a reduction of silt content, and that these changes were most pronounced in the area dredged for cockles. Sediment characteristics only returned to pre-impact conditions 8-11 years after the suction dredging. The authors concluded that suction dredging of *Cerastoderma edule* had long lasting effects on the recruitment of bivalves (particularly the target species *Cerastoderma edule*, but also *Limecola balthica*) in sandy parts of the Wadden Sea basin.

Initial sediment reworking by suction dredging especially during autumn storms) probably caused loss of fine silts and then negative feedback processes appeared to follow that prevented the accumulation of fine-grained sediments conducive to bivalve settlement.

Limecola balthica thrives in low energy environments such as estuaries (Tebble, 1976) where the substratum has a high proportion of fine sediment. Green (1968) recorded that towards the mouth of an estuary where sediments became coarser and cleaner, *Limecola balthica* was replaced by another tellin species, *Tellina tenuis*. Kraan *et al.* (2007) noted that a reduction in fine silts following cockle dredging was believed to have led to decreased recruitment of *Limecola balthica*. These effects persisted for over eight years after dredging (Piersma *et al.*, 2001). Newell (1965) (cited in Green, 1968) noted that *Limecola balthica* populations in the Thames Estuary, UK, were denser where the grade of deposit was finer, possibly due to greater food availability.

Experimental relaying of mussels on intertidal fine sand sediments increased fine sediment proportions and led to colonisation by *Capitella capitata* (Ragnarsson & Rafaelli, 1999). Experimental studies have shown that *Capitella capitata* have increased in abundance where there has been a 2-3 cm layer of fine resuspended and re-settled sediment (McCall, 1977). However the settlement may be due to enhanced food supply rather than the increase in fine sediments alone.

Eteone longa has wide sediment preferences, it would be able to tolerate an increase in coarse sediments within the habitat envelope. The presence of this species on a range of coarse substrata/sediments indicate that it would be able to tolerate (but possibly with population impacts) an increase in sediment coarseness (e.g. where shells and larger sediments accumulate). However, a transition to a fully coarse sediment type is likely to negatively impact this species as the habitat becomes sub-optimal. Degraer *et al.* (2006) indicate that a change to a very fine sediment would, however, exclude this species.

Pygospio elegans prefers fine sediments such as sand and mud; increased sediment coarseness is likely to render sediments unsuitable for this species. Empirical evidence supporting this view is provided by Bolam (1999) where experimental manipulation of sediments by implanting macroalgae mats led to increased fine sediment fractions (with associated increased organic and water content) which led to the establishment of *Pygospio elegans*.

Sensitivity assessment. The character of the habitat is largely determined by the sediment type, changes to this would lead to habitat re-classification. The addition of coarse sand particles or fine particles in sufficient quantities would lead to the development of a different habitat type. Changes in sediment characteristics can lead to changes in community structure. An increase in coarse sediments would lead to the development of a community typical of mixed sediments, clean sands and/or gravels depending on the degree of change. In general an increase to very coarse sediments may favour some amphipod species rather than *Cerastoderma edule*, *Limecola balthica*, and the associated burrowing polychaetes and sessile tube-dwelling polychaetes. This change would alter the character of the biotope present leading to re-classification, biotope resistance is assessed as 'None' and, as the change is permanent, resilience is assessed as 'Very Low'. Biotope sensitivity is therefore 'High'.

The presence of the characterizing species in muddy sands indicates that sediments with fine fractions provide suitable habitat and the characterizing and associated species are also found in mud habitats (e.g. *Cerastoderma edule*, *Capitella* sp., *Pygospio elegans*, *Eteone* sp.). The majority of the species were therefore considered to have 'High' resistance to a change to a mud sediment. However as mudflat habitats are more suitable for deposit feeders than suspension feeders,

Cerastoderma edule was considered likely to experience a reduction in habitat suitability following a change in sediment type, a reduced abundance of this species is likely to facilitate colonization by other species typically associated with mud habitats, resulting in a change in assemblage structure and biotope reclassification. Recovery will depend on the degree of effect and site specific habitat forming processes, including sediment supply and hydrodynamics. On many shores, areas of different sediment type are found and the extent and location of these may be fairly dynamic, biotope recovery is, however, assessed as 'Very low' as the change at the pressure benchmark is considered to be permanent. Sensitivity was, therefore, assessed as 'High'.

Habitat structure changes - removal of substratum (extraction)

None

Q: High A: High C: High

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Sedimentary communities are likely to be highly intolerant of substratum removal, which will lead to partial or complete defaunation, expose underlying sediment which may be anoxic and/or of a different character or bedrock and lead to changes in the topography of the area (Dernie *et al.*, 2003). Any remaining species, given their new position at the sediment / water interface, may be exposed to conditions to which they are not suited, i.e. unfavourable conditions. Recovery by infilling will depend on local factors including the mobility of sediments, sediment supply, hydrodynamics and the spatial scale of the area affected (Van Hoey *et al.* 2008).

The extraction of sediment would remove the characterizing species and all associated species present, including *Cerastoderma edule*, which is found to a depth of 5 cm (Tebble, 1976) and Nephtyid species and other polychaetes, such as *Scoloplos armiger* and *Pygospio elegans* that burrow between 5 and 20 cm into the sediment (Schüttler, 1982; Pedersen, 1991; Kruse *et al.*, 2004). Undamaged individuals of *Cerastoderma edule* displaced to the sediment surface may survive and re-bury (Coffen-Smout & Rees, 1999).

Direct evidence of recovery by *Limecola balthica* following substratum loss is given by Bonsdorff (1984). Bonsdorff (1984) studied the recovery of a *Limecola balthica* (as *Macoma balthica*) population in a shallow, brackish bay in SW Finland following the removal of the substratum by dredging in the summer of 1976. Recolonization of the dredged area by *Limecola balthica* began immediately after the disturbance to the sediment and by November 1976, the *Limecola balthica* population had recovered to 51 individuals/m². One year later there was no detectable difference in the *Limecola balthica* population between the recently dredged area and a reference area elsewhere in the bay. In 1976, 2 generations could be detected in the newly established population indicating that active immigration of adults was occurring in parallel to larval settlement. In 1977, up to 6 generations were identified, giving further evidence of active immigration to the dredged area.

Sensitivity assessment. Extraction of 30 cm of sediment will remove the characterizing biological component of the biotope and sediments. The resistance of the habitat to extraction is assessed as 'None' as sediment is removed: the depth of remaining sediments and their character will be site-specific. Recovery will depend on local factors including hydrodynamics, sediment supply and sediment mobility and the spatial scale affected. Resilience is assessed as 'Medium' as sediment infilling may be rapid in intertidal areas, however, recruitment of the characterizing *Cerastoderma edule* is episodic (see resilience section). Biotope sensitivity is therefore assessed as 'Medium'. If sediments do not return to the previous condition, larval recolonization may be inhibited (see physical change pressures).

Abrasion/disturbance of the surface of the substratum or seabed

Medium

Q: High A: High C: Medium

High

Q: High A: Low C: Medium

Low

Q: High A: Low C: Medium

Muddy sand sediments, in general, tend to be cohesive although high levels of water content will reduce this and destabilise sediments. Sediment cohesion provides some sediment stabilisation to resist erosion following surface disturbance. Species associated with muddy sands/sandy muds are infaunal and hence have some protection against surface disturbance, although tubes of sedentary polychaetes, such as *Pygospio elegans*, may project above the sediment surface and damage to these would require repair. *Cerastoderma edule* has short siphons and requires contact with the surface for respiration and feeding. Surface compaction can collapse burrows and reduce the pore space between particles, decreasing penetrability and reducing stability and oxygen content (Sheehan, 2007). Trampling (3 times a week for 1 month) associated with bait digging reduced the abundance and diversity of infauna (Sheehan, 2007; intertidal muds and sands). However, Cooke *et al.* (2002) found that trampling associated with bait digging had little effect on infaunal species composition (intertidal muddy sands).

Chandrasekara and Frid (1996; cited in Tyler-Walters & Arnold, 2008; who inferred the community as intertidal mud from the communities present) found that along a pathway heavily used for five summer months (ca 50 individuals a day) some species (e.g. *Capitella capitata* and *Scoloplos armiger*) reduced in abundance while others increased in abundance, probably due to rapid recruitment and growth of more opportunistic species, even though their population experienced mortality. Recovery took place within 5-6 months. Juveniles and adults of *Scoloplos armiger* stay permanently below the sediment surface and freely move without establishing burrows. While juveniles are only found a few millimeters below the sediment surface, adults may retreat to 10 cm depth or more (Reise, 1979; Kruse *et al.*, 2004) and are likely to be more protected. The egg cocoons are laid on the surface and hatching time is 2-3 weeks during which these are vulnerable to surface abrasion.

Rossi *et al.* (2007) conducted experimental trampling on a mudflat (5 people, 3-5 hours, twice a month between March and September). Mobile fauna were not affected; however, the abundance of adult *Cerastoderma edule* was sharply reduced, probably due to the trampling directly killing or burying the animals, resulting in asphyxia. However, no effect was observed on small (<12 mm) individuals of *Cerastoderma edule*. The authors suggested that this was because the experiment was conducted in the reproductive season for these species and hence there were juveniles present in the water column to replace individuals displaced by trampling. The lack of observed effect was therefore due to continuous recruitment and replacement of impacted individuals.

Sensitivity assessment. Abrasion at the surface is likely to damage a proportion of the population shallow buried bivalves (*Cerastoderma edule* and *Limecola balthica*) and soft-bodied species that live on or very close to the surface (*Pygospio elegans* and *Capitella capitella*). The level of damage and mortality will depend on the force exerted. Biotope resistance is assessed as 'Medium' and resilience is assessed as 'High' so that biotope sensitivity is therefore assessed as 'Low'

Penetration or disturbance of the substratum subsurface

Low

Q: High A: High C: High

Medium

Q: High A: High C: High

Medium

Q: High A: High C: High

In contrast to rocky shores, few soft sediment fauna are found on the sediment surface at low tide.

As a consequence, harvesting of soft sediment fauna requires the physical disturbance of the substratum. Moreover, these habitats tend to extend over large areas which, coupled with their low topography and the structure of the substratum, makes them amenable to extensive mechanical harvesting (Kaiser *et al.*, 2001). Towed demersal gears, such as beam trawls, otter trawls, scallop dredges, could be deployed in intertidal sandy and muddy habitats depending on the tidal regime and the morphology of the coastline (Hall *et al.*, 2008). Due to commercial interest and the accessibility of intertidal areas, a number of academic studies have assessed the effects of these fisheries, including the impact of sediment disturbance on the species found within this biotope. This assessment is divided into three sections; considering impacts on the key characterizing *Cerastoderma edule*; associated species and the sedimentary habitat. Changes to sediment are also relevant to the physical change assessments and the evidence for impacts of substratum changes and the impact on the biotope is considered more fully in that section.

Impacts on Cerastoderma edule.

In the Burry Inlet, Wales, intertidal tractor towed cockle harvesting led mechanical cockle harvesting in muddy sand reduced the abundance of *Cerastoderma edule* by ca 34%. Populations of *Cerastoderma edule* had not recovered their original abundance after 174 days (Ferns *et al.* 2000). Hall and Harding (1997) studied the effect of suction and tractor dredging for cockles on non-target benthic fauna in the Solway Firth, Scotland where sediments contained 60-90% silt/clay in the more sheltered areas. The results showed that suction dredging resulted in significantly lower mean species numbers (by up to 30%) and mean numbers of individuals (up to 50%) and in the abundance of 3 of the 5 dominant species. The faunal structure of the dredged plots recovered (i.e. approached that of the undisturbed control plots) by 56 days. The results of the tractor dredge experiments showed fewer effects than the suction dredging (no significant effect on the number of species or individuals). The authors concluded that mechanical harvesting methods imposed high levels of mortality on non-target benthic fauna but that the recovery of disturbed sites was rapid and that the overall effects on populations were low. Although the results suggested that tractor dredging had less impact than suction dredging the authors proposed this may have been due to differences in the timing of the experiments (May-July suction dredging; July-September tractor dredging). They concluded that although significant mortality of *Cerastoderma edule* and other infauna occurred, recovery was rapid and the overall effects on populations were low. Hall & Harding (1997) found that abundance had returned to control levels within about 56 days and Moore (1991) also suggested that recovery was rapid. Rostron (1995) carried out experimental dredging of sandflats with mechanical cockle dredge. Two distinct sites were sampled; Site A: poorly sorted fine sand with small pools and *Arenicola marina* casts with some algal growth, and Site B: well sorted fairly coarse sand, surface sediment well drained and rippled as a result of wave activity. At both sites, *Cerastoderma edule* reduced after dredging but recovery was rapid at Site B (no difference between control and experimental plots after 14 days), whilst at Site A significant reduction in numbers compared with the control were still apparent up to six months post-dredging.

With respect to displacement, cockles are capable of burrowing rapidly into the substratum and >50% burrowed into the substratum within 1 hour in experimental trials (Coffen-Smout & Rees, 1999), although this rate was inhibited by prior disturbance. Brock (1979) reported that 80% began to burrow within 60 min and 50% had successfully burrowed into sediment within 60 min. He also noted that young cockles could burrow quickly, and were nearly buried within 5 min. Hand-raking for cockles was shown not to influence the re-burial rate of cockles in Strangford Lough, Northern Ireland (McLaughlin *et al.* 2007).

Impacts on associated species

Experiments found that suction dredging to remove cockles led to a decline in associated species richness and species abundance (Hall & Harding, 1998). In contrast, tractor dredging did not lead to significant, observable effects on non-target species. Recovery was tracked following the disturbance, after 56 days there was little difference between dredge and control sites. This rapid recovery coincided with annual recruitment supporting recovery (Hall & Harding, 1998). Several studies have assessed the impact of cockle dredging on non-target species including *Limecola balthica*. Piersma *et al.* (2001) showed that after suction dredging for cockles (*Cerastoderma edule*) in the Dutch Wadden Sea, the abundance of *Limecola balthica* declined for eight years. Declines of bivalve stocks were caused by low rates of settlement in the fished areas. Hiddink (2003) also reported a significant negative effect of cockle dredging on the density of 0-group *Limecola balthica* (as *Macoma balthica*), which persisted for one year after dredging, likely due to the habitat being less suitable following dredging. Kraan *et al.* (2007) also showed that the deep disturbance from cockle dredging led to decreased densities of *Limecola balthica* on intertidal mudflats flats (sand and muddy sand sediment) in the Dutch Wadden Sea.

Bergman and Hup (1992) found that worm species (including *Scoloplos armiger*) showed no change in total density after trawling a subtidal habitat. Conversely, a later study by Bergman and Santbrink (2000) found that the direct mortality of *Scoloplos armiger* from a single passage of a beam trawl in subtidal silty grounds was 18% of the population. Rostron (1995) undertook experimental dredging of sandflats with a mechanical cockle dredger, including a site comprised of stable, poorly sorted fine sands with small pools and *Arenicola marina* casts with some algal growths. At this site, post-dredging *Scoloplos armiger* had disappeared from some dredged plots. Ferns *et al.* (2000) used a tractor-towed cockle harvester, to extract cockles from intertidal plots of muddy sand and clean sand, to investigate the effects on non-target organisms; 31% of the population of *Scoloplos armiger* (initial density of 120 per m²) were removed. Populations of *Scoloplos armiger* remained significantly depleted in the area of muddy sand for more than 50 days after harvesting. Ball *et al.* (2000) found that species including *Scoloplos armiger* showed a significant decrease in abundance of between 56-27% after 16 months of otter trawling at a previously unfished Scottish sea loch. Chandrasekara and Frid (1996, cited in Tyler-Walters & Arnold, 2008) found that along a pathway heavily used for five summer months (ca. 50 individuals day⁻¹), *Scoloplos armiger* reduced in abundance. Recovery took place within 5-6 months. These studies suggest that *Scoloplos armiger* is likely to be impacted by sediment disturbance and that recovery to previous densities may require more than two years.

A number of studies have found that the abundance of the polychaete *Pygospio elegans* is reduced by simulated cockle dredging (Hall & Harding, 1998; Moore, 1990; Ferns *et al.*, 2000; Rostron, 1995). Ferns *et al.* (2000) found that tractor towed cockle harvesting removed 83% of *Pygospio elegans* (initial density 1850/ m²). In muddy sand habitats, *Pygospio elegans* had not recovered to the original abundance after 174 days (Ferns *et al.*, 2000). Rostron (1995) also found that *Pygospio elegans* had not recovered to pre-dredging numbers after six months. Conversely, Hall & Harding, (1998) found that abundance of *Pygospio elegans* increased significantly over 56 days following suction dredging. *Pygospio elegans* inhabits a fragile tube that projects above the sediment surface and is probably more vulnerable to physical disturbance and abrasion than other, more deeply buried, infaunal species.

Rees, 1978, (cited in Hiscock *et al.*, 2002), assessed pipe-laying activities. The pipe was laid in a trench dug by excavators and the spoil from the trenching was then used to bury the pipe. The trenching severely disturbed a narrow zone, but a zone some 50 m wide on each side of the

pipeline was also disturbed by the passage of vehicles. The tracked vehicles damaged and exposed shallow-burrowing species such as *Cerastoderma edule* and *Limecola balthica*, which were then preyed upon by birds. During the construction period, the disturbed zone was continually re-populated by mobile organisms, such as the mud snail *Hydrobia ulvae*. Post-disturbance recolonisation was rapid. Several species, including the polychaetes, *Eteone longa*, and *Scoloplos armiger* were recruited preferentially to the disturbed area.

Impacts on sediment

Tractor dredging leaves visible tracks in the sediment, which can act as lines for erosion and accelerate erosion of the sediment (Moore, 1991; Gubbay & Knapman, 1999). In most cases, the subsequent settlement was good especially in areas of previously high population density; however, Franklin and Pickett (1978) noted that subsequent spat survival was markedly reduced. Hall & Harding, (1998), assessed the effects of tractor towed cockle dredgers on sediment erodibility. Effects were short-term, with dredged sediments having greater erodibility (lower shear stress) following dredging which increased over 48 hours back to the levels observed in the undredged plots. Cotter *et al.*, (1997) also noted that dredge tracks not clearly visible after 1 day, demonstrating rapid infilling.

Sensitivity assessment. The available evidence indicates that small patches of physical disturbance are likely to be in-filled by adult cockle movement, large patches will recover through larval recruitment, which again is subject to many factors, and may be improved by the removal of adult cockles. Biotope resistance is assessed as 'Low' based on loss of characterizing species *Cerastoderma edule* and associated species. Resilience is assessed as 'Medium' to take account of recruitment variability and return of normal age structure. Sensitivity is therefore categorized as 'Medium'.

Changes in suspended solids (water clarity)

High

Q: High A: Medium C: High

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: High

Increasing total particulate concentrations have been shown to decrease clearance rates and increase pseudofaeces production in *Cerastoderma edule* (Navarro *et al.* 1992; Navarro & Widdows, 1997). Filtration rates increased with particulate concentration until 300 mg/l at which concentration filtration rates abruptly declined. Pseudofaeces production was triggered by concentrations of total particulate matter of 1.5 mg/l (Navarro *et al.*, 1992) or 4.8 mg/l (Navarro & Widdows, 1997). However, the absorption efficiency remained independent of particulate concentration over a large range but reduced at concentrations above 250 mg/l (Navarro & Widdows, 1997). Navarro and Widdows (1997) concluded that *Cerastoderma edule* was well adapted to living in turbid environments such as intertidal mudflats. Increased siltation and suspended sediment concentration result in increased pseudofaeces production and concomitant loss of energy and carbon as mucus. Therefore, *Cerastoderma edule* probably has a low intolerance to increased suspended sediment.

Increasing turbidity may reduce phytoplankton productivity and hence decrease food availability, however, *Cerastoderma edule* is capable of ingesting organic seston and is adapted to life in sedimentary and estuarine conditions where turbidity is high (Navarro & Widdows, 1997). Therefore, *Cerastoderma edule* is probably tolerant to changes in turbidity (Tyler-Walters, 2007).

A decrease in turbidity and hence increased light penetration may result in increased phytoplankton production and hence increased food availability for suspension feeders, including

Cerastoderma edule. Therefore, reduced turbidity may be beneficial. In areas of high suspended sediment, a decrease may result in improved condition and recruitment due to a reduction in the clogging of filtration apparatus of suspension feeders and an increase in the relative proportion of organic particulates. However, a decrease in suspended organic particles in some areas may reduce food availability resulting in lower growth or reduced energy for reproduction. Infauna not directly affected but may be indirectly affected by changes in sediment composition from increased deposition or reduction in biodeposition from *Cerastoderma edule* from reduced clearance.

Limecola balthica is known to practice two alternative modes of feeding. It either holds its feeding organ, the siphon, at a fixed position just above the sediment surface to filter out food particles suspended in the overlying water, or extends and moves its siphon around on the sediment above it to vacuum up deposited food particles (Peterson & Skilleter, 1994). Facultative switching between the modes of feeding in *Limecola balthica* is directly affected by food availability in the over-lying water (Lin & Hines, 1994). In turn, changes in feeding mode from suspension to deposit feeding directly affects burial depth. In the laboratory, Lin & Hines (1994) observed specimens of *Limecola balthica* kept in estuarine water supplemented with 75 µg/l of algae to maintain a deeper burial position whilst suspension feeding, than those without an enhanced diet who deposit fed. Thus, an increase of material in suspension will favour suspension feeding by *Limecola balthica* and indirectly reduce its vulnerability to lethal and sub-lethal siphon browsing by fish and decapods. *Limecola balthica* is therefore assessed as 'tolerant' with the potential for growth and reproduction to be enhanced by the increased food supply.

Sensitivity assessment. A decrease in turbidity and hence increased light penetration may result in increased phytoplankton production and hence increased food availability for suspension feeders, including *Cerastoderma edule*. Therefore, reduced turbidity may be beneficial. In areas of high suspended sediment, a decrease may result in improved condition and recruitment due to a reduction in the clogging of filtration apparatus of suspension feeders and an increase in the relative proportion of organic particulates. However, a decrease in suspended organic particles in some areas may reduce food availability for deposit feeders resulting in lower growth or reduced energy for reproduction. Where increased turbidity results from organic particles then subsequent deposition may enhance food supply for deposit feeders within the biotope such as *Limecola balthica* and deposit feeding polychaetes. Alternatively, if turbidity results from an increase in suspended inorganic particles then energetic costs may be imposed on these species as sorting and feeding becomes less efficient reducing growth rates and reproductive success. Lethal effects are considered unlikely given the occurrence of *Cerastoderma edule* and other associated species in estuaries where turbidity is frequently high from suspended organic and inorganic matter. Resistance and resilience are therefore assessed as 'High' and the biotope is considered to be 'Not sensitive'.

Smothering and siltation rate changes (light)

Medium

Q: High A: High C: High

High

Q: High A: Low C: Medium

Low

Q: High A: Low C: Medium

Cerastoderma edule has short siphons and needs to keep in contact with the surface of the sediment. Richardson et al. (1993) reported that they burrow quickly to the surface if covered by 2 cm of sediment (under laboratory or field conditions) when emerged (45% of cockles emerged onto the surface in light and 60% in darkness). In light the cockles quickly re-burrow, however, in darkness they move across the substratum, partly to increase the distance between neighbours. Richardson et al. (1993) suggested that surface movement in darkness might be a response to

coverage from siltation.

Bait digging (for large polychaete worms) disturbs the sediment down to a depth of 30cm (Jackson & James, 1979) and results in repositioning of species when the extracted sediment is placed back in holes or smothering where sediment is piled on the surface. Intensification of bait digging on intertidal flats on the north Norfolk coast for lugworm (*Arenicola marina*) and ragworm (*Hediste diversicolor*) was associated with declines in the *Cerastoderma edule* populations (Jackson & James, 1979). Experimental simulation of bait digging (sediment dug over to a depth of 30cm with a garden fork) led to high mortalities of cockles in dug areas rather than undug areas (48% mortality in 9 days to a maximum of 85% after 11 days) probably due to smothering (Jackson & James, 1979). The observation was tested experimentally in the laboratory by burying 3 size-classes of cockles at 0, 5 or 10cm depth in a mix of oxidated and deeper anoxic sands (mixed as a ratio of 3:1) was used as the sediment. Movements were recorded after 24, 48 and 72 hours. When buried to 5 cm depth most cockles returned to the surface but few were able to reposition to the surface if buried at 10cm depth. None had died after 72 hours. Additional burial experiments under 10 cm of sediment assessed movement and survival after 3, 6 and 9 days in two sediment types (a mix of surface mud and sand in two ratios 9:1 and 1:9). The movement towards the surface was slower in the predominantly muddy sediment and all cockles died between 3 and 6 days. Substantial mortality resulted in the predominantly sandy mixture although some cockles were able to move towards the surface and survive for 9 days.

Gam *et al.* (2010) compared population dynamics and secondary production of *Cerastoderma edule* between Merja Zerga on the Moroccan Atlantic coast (close to the species southerly limit) and Arcachon Bay on the French Atlantic coast. During their study of recruitment in January 2007, mass mortalities were observed in both adult and juvenile cockles and this was attributed to high sand bank displacements in the previous year, which partly covered and smothered the cockle population.

Limecola balthica is able to burrow both vertically and horizontally through the substratum. It is likely that *Limecola balthica* is not sensitive to smothering by a layer of sediment 5 cm thick as it is a mobile species able to burrow upwards and surface from a depth of 5 - 6 cm (Brafield & Newell, 1961; Brafield, 1963; Stekoll *et al.*, 1980). Turk and Risk (1981) investigated the effect of experimentally induced sedimentation (through fences and boxes that induced sediment deposition on intertidal mudflats in the Bay of Fundy), of 1-3.5cm at a rate of 1.9-10.2 cm/month. The results showed that *Limecola balthica* was generally unaffected.

The associated species *Pygospio elegans* is limited by high sedimentation rates (Nugues *et al.*, 1996) and the species does not appear to be well adapted to oyster culture areas where there are high rates of accumulation of faeces and pseudo faeces (Sornin *et al.*, 1983; Deslous-Paoli *et al.*, 1992; Mitchell, 2006 and Bouchet & Sauriau 2008). *Pygospio elegans* is known to decline in areas following re-deposition of very fine particulate matter (Rhoads & Young, 1971; Brenchley, 1981). Experimental relaying of mussels on intertidal fine sands led to the absence of *Pygospio elegans* compared to adjacent control plots. The increase in fine sediment fraction from increased sediment deposition and biodeposition alongside possible organic enrichment and decline in sediment oxygen levels was thought to account for this (Ragnarsson & Rafaelli, 1999).

Mobile and/or burrowing species (including molluscs and polychaetes such as *Hydrobia ulvae*, *Eteone longa* and *Scoloplos armiger*) are generally considered to be able to reposition following periodic siltation events or low levels of chronic siltation. Field experiments where 10 cm of sediment were placed on intertidal sediments to investigate the effects of the beneficial use of

dredged materials found that the abundance of *Hydrobia ulvae* had returned to ambient levels within 1 week (Bolam et al. 2004). However, survival depends on several factors. The snail can only burrow up through certain sorts of sediment. If the silt content of the smothering sediment is high and the water content low then it is unlikely that the surface will be regained from 5 cm down. Looser sediment with high water and low silt content can be negotiated quite rapidly. The surface is generally regained within a day. If the surface cannot be regained then *Hydrobia ulvae* can survive burial for quite extended periods although this is highly temperature dependent. Temperatures of 20°C result in all individuals dying after 10 days. Survival is much better at lower temperatures. It is thought that oxygen stress is the cause of mortality (Jackson, 2000).

Sensitivity assessment. Biotope resistance based on the characterizing *Cerastoderma edule* is assessed as having 'Medium' resistance to siltation, (as many would be able to survive and re-emerge from a 5cm depth of sediment). Resilience is assessed as 'High' based on adult migration and repopulation by larvae. Many of the associated species are also likely to reposition although *Pygospio elegans* may be more sensitive.

Smothering and siltation rate changes (heavy)

Low

Q: High A: High C: Medium

Medium

Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Cerastoderma edule has short siphons and needs to keep in contact with the surface of the sediment. Bait digging (for large polychaete worms) disturbs the sediment down to a depth of 30 cm (Jackson & James, 1979) and leads to repositioning within sediment or burial from piled sediments. Intensification of bait digging on intertidal flats on the north Norfolk coast for lugworm (*Arenicola marina*) and ragworm (*Hediste diversicolor*) was associated with declines in the *Cerastoderma edule* populations (Jackson & James, 1979). Experimental simulation of bait digging (sediment dug over to a depth of 30 cm with a garden fork) led to high mortalities of cockles in dug areas rather than undug areas (48% mortality in 9 days to a maximum of 85% after 11 days) probably due to smothering (Jackson & James, 1979). The observation was tested experimentally in the laboratory by burying 3 size-classes of cockles at 0, 5 or 10 cm depth in a mix of oxidated and deeper anoxic sands (mixed as a ratio of 3:1) was used as the sediment. Movements were recorded after 24, 48 and 72 hours. When buried to 5 cm depth most cockles returned to the surface but few were able to reposition to the surface if buried at 10cm depth. None had died after 72 hours. Additional burial experiments under 10 cm of sediment assessed movement and survival after 3, 6 and 9 days in two sediment types (a mix of surface mud and sand in two ratios 9:1 and 1:9). The movement towards the surface was slower in the predominantly muddy sediment and all cockles died between 3 and 6 days. Substantial mortality resulted in the predominantly sandy mixture although some cockles were able to move towards the surface and survive for 9 days.

Maurer *et al.* (1986) studied the effects of dredged material on the vertical migration and mortality of four species of benthic invertebrates (including two polychaetes) and reported that the intolerance of species to smothering was influenced by the nature of the sediment. They predicted that some individuals of both the polychaete species studied (*Nereis succinea* and *Scoloplos fragilis*) would be capable of vertical migration through 0.9 m of sediment if that sediment was indigenous to their usual habitat (Marshall, 2008).

Field experiments where 10 cm of sediment were placed on intertidal sediments to investigate the effects of the beneficial use of dredged materials found that the abundance of *Hydrobia ulvae* had returned to ambient levels within 1 week (Bolam et al. 2004). It is not clear whether this species could reposition after 30cm of sediment were placed on sediments.

Sensitivity assessment. The addition of 30 cm of sediment would prevent *Cerastoderma edule* and *Limecola balthica* from extending siphons to the surface. It is unlikely that these species could emerge from this depth of sediment although some individuals may survive and sediment may be rapidly removed by tide and wave action. It is likely, however, that there would be considerable mortality of the characterizing *Cerastoderma edule* and biotope sensitivity is based on this species. Resistance is assessed as 'Low' and resilience as 'Medium' (based on episodic recruitment). Sensitivity is, therefore, assessed as 'Medium'. The sensitivity of the associated species is unclear. Although some polychaetes may be able to reposition following sedimentation at the pressure benchmark this will depend on the characteristics of the overburden and sedentary species such as *Pygospio elegans* are likely to suffer high levels of mortality.

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
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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
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No evidence.

Underwater noise changes	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR
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Not relevant.

Introduction of light or shading	High Q: High A: Low C: Medium	High Q: High A: High C: High	Not sensitive Q: High A: Low C: Medium
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The key characterizing and associated species do not photosynthesize and are unlikely to be directly affected by shading or increased light levels. The abundance and production of microphytobenthos in sediments may be impacted by shading and this may have indirect effects on secondary production by animals that feed on these. The key characterizing species *Cerastoderma edule* feeds on suspended seston and is unlikely to be directly affected by localised changes in microphytobenthos production.

Cerastoderma edule carries about 60 eyes on the sensory siphonal tentacles (Barber & Wright 1968). The basic response to light in bivalves is defensive with responses including digging, closing of valves and siphonal withdrawal (Morton, 2008). Changes in light levels may also simulate other behavioural responses and emergence of cockles in response to darkness has been observed (Richardson *et al.*, 1993). The polychaetes found within the biotope including *Eteone longa*, *Capitella capitata* and others contain photoreceptors (Purschke *et al.*, 2006) and are likely to perceive changes in light levels.

Light levels may act as cues for reproduction (although temperature also regulates reproduction for many species) supporting synchronised spawning for species with external fertilisation. No evidence was found to suggest that light levels are an important reproductive cue for characterizing and associated species.

Sensitivity assessment. Light penetration into sediments is limited to the surface layers and permanently buried infauna such as *Scoloplos armiger* are unlikely to be affected by changes in light levels. The characterizing *Cerastoderma edule* and other species present can perceive light but the effects of changes in light level and shading or the duration of light and darkness are not clear. As It is considered unlikely that changes in light levels would have significant effects on the key and associated species, biotope resistance is assessed as 'High' and resilience as 'High' (by default) and the biotope is considered to be 'Not sensitive'.

Barrier to species movement

High

Q: Low A: NR C: NR

High

Q: High A: High C: High

Not sensitive

Q: Low A: Low C: Low

No direct evidence was found to assess this pressure. As the larvae of *Cerastoderma edule* and *Limecola balthica* are planktonic and are transported by water movements, barriers that reduce the degree of tidal excursion may alter larval supply to suitable habitats from source populations. However the presence of barriers may enhance local population supply by preventing the loss of larvae from enclosed habitats. Species that do not have a pelagic larval stage such as *Scoloplos armiger* or those that alternate between pelagic and benthic dispersal stages such as *Pygospio elegans* and *Capitella capitata* are less likely to be impacted by this pressure. As both the key characterizing species are widely distributed and have larvae capable of long distance transport and long residence times in the water column, resistance to this pressure is assessed as 'High' and resilience as 'High' by default. This biotope is therefore considered to be 'Not sensitive'.

Death or injury by collision

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

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

Visual disturbance

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

No evidence found. As the species characterizing this biotope are not primary producers, have limited visual acuity and inhabit turbid, coastal waters and estuaries where light penetration may be limited the pressure is assessed as 'Not relevant' to this biotope.

Biological Pressures

Resistance

Resilience

Sensitivity

Genetic modification & translocation of indigenous 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

The key characterizing and associated species within this biotope are not cultivated or translocated. This pressure is therefore considered 'Not relevant' to this biotope group.

Due to long distance transport of pelagic larvae populations of the key characterizing species, *Cerastoderma edule*, may be interconnected and populations are not genetically isolated, with

populations such as those at Pembroke showing mixing between British and Irish populations (Coscia *et al.*, 2013). It should be noted that where local hydrodynamics prevent larval transport some genetically isolated populations may occur, as in the Burry Inlet, south Wales (Coscia *et al.*, 2013).

Introduction or spread of invasive non-indigenous species

Low

Q: High A: High C: Low

Very Low

Q: Low A: NR C: NR

High

Q: Low A: Low C: Low

Intertidal flats may be colonized by the invasive non-indigenous species *Crepidula fornicata* and *Magallana gigas*. The two species have not only attained considerable biomasses from Scandinavian to Mediterranean countries but have also generated ecological consequences such as alterations of benthic habitats and communities, or changes to the food chain (OSPAR, 2009).

In the Wadden Sea, the Pacific oyster *Magallana gigas* has colonized intertidal flats (Smaal *et al.*, 2005). This species may consume larvae including the pelagic larvae of *Cerastoderma edule* and *Limecola balthica* and other species reducing recruitment (Smaal *et al.*, 2005). Troost *et al.* (2009) investigated whether *Magallana gigas* had a competitive feeding advantage over *Cerastoderma edule* and concluded that differences in feeding current characteristics were small and not considered to lead to significant differences in feeding efficiency. The most severe effects are likely to occur from impacts on sediment, where *Magallana gigas* create reefs on sedimentary flats that will prevent recruitment of juveniles and will restrict access of infauna to the sediment-water interface impacting respiration and feeding.

The Manila clam (*Tapes philippinarium*), which was introduced to Poole Harbour for aquaculture in 1998, has become a naturalised population on the intertidal mudflats (occurring at densities of 60 clams/m² in some locations within the harbour (Jensen *et al.* 2007, cited in Caldow *et al.* 2007). Densities of *Cerastoderma edule* and *Abra tenuis* had increased since the introduction of the Manila clam although the abundance of *Scrobicularia plana* and *Limecola balthica* declined (Caldow *et al.*, 2005), although the decline of these species may have been caused by tri-butyl tin pollution (Langston *et al.* 2003) and may have facilitated the naturalization of the Manila clam.

The burrowing lifestyle of *Eteone longa* and other infaunal polychaetes may confer some protection from changes to the sediment surface and may provide some new habitat (as this species has been found among oyster banks).

The predatory veined whelk (*Rapana venosa*) and *Hemigrapsus takinei* are not established in the UK (although *Hemigrapsus takinei* has been recorded at two locations) could become significant predators of *Cerastoderma edule* and other species associated with the biotope in the future.

Sensitivity assessment. Intertidal muddy sands may be exposed to invasive species which can alter the character of the habitat (primarily *Crepidula fornicata* at the sublittoral fringe and *Magallana gigas*) leading to re-classification of this biotope, the biotope is considered to have 'Low' resistance and 'Very Low' recovery (unless invasive species are removed). Biotope sensitivity is therefore assessed as 'High'.

Introduction of microbial pathogens

Low

Q: High A: High C: High

Medium

Q: High A: Low C: High

Medium

Q: High A: Low C: Medium

A recent review of parasites, pathogens and commensals identified a range of agents impacting European cockles, including 50 conditions affecting *Cerastoderma edule* (Longshaw & Malham, 2013). Cockles are hosts to viruses, bacteria, fungi, Apicomplexa, Amoeba, Ciliophora, Perkinsozoa, Haplosporidia, Cercozoa, Turbellaria, Digenea, Nematoda, Crustacea and Nemertea. Mortalities are associated particularly with digeneans and some protistan infections; parasites may limit growth, reduce fecundity and alter burrowing behaviour (Longshaw & Malham, 2013). A number of examples of conditions associated with mass mortalities of *Cerastoderma edule* are presented below. Parasites and disease are more likely to cause mortalities in populations that are subject to suboptimal conditions or other stressors such as hot summers or cold winters (Longshaw & Malham, 2013). Experimental infection of *Cerastoderma edule* with a trematode parasite showed that effects differed depending on habitat conditions (Wegeberg & Jensen, 2003). Infected *Cerastoderma edule* reared in sub-optimal conditions lost more body weight than infected cockles in more optimal habitats and did not regain condition when placed in higher shore habitats where immersion and food supply was limited. Infected cockles placed on lower shore sites with longer emersion times regained condition despite the infection and were equivalent to controls. The impact of trematodes is therefore mediated by habitat conditions and in some instances may have no effect (Wegeberg & Jensen, 2003).

Infestation by a trematode parasite *Cercaria cerastodermae* impairs the burrowing ability of *Cerastoderma edule* and was identified as the likely cause of a mass mortality of cockles in Scandinavian waters in 1991 (Jonsson & André, 1992). Another trematode parasite *Gymnophallis choledochus* may castrate *Cerastoderma edule*, reducing reproduction and recruitment and indirectly leading to population declines (Thieltges, 2006).

An unidentified amoeba, measuring 18–20 mm in diameter, was described from the sub-epithelial gill tissues of *Cerastoderma edule* from Portugal (Azevedo, 1997). The amoeba was associated with haemocytic infiltration and necrosis of host cells. Affected cockles were found gaping at the surface and the infection was considered to be responsible for mass mortalities.

Cockles also suffer from disseminated neoplasia—a leukaemia like disease associated with mass mortalities. *Cerastoderma edule* from Ireland have been reported to be especially susceptible (Barber *et al.*, 2004). High mortalities of cockles observed in north west Spain in 1997 were associated with a higher prevalence (up to 84%) of disseminated neoplasia compared to control areas (4% prevalence) not experiencing mortality (Villalba *et al.* 2001).

Sensitivity assessment. The available evidence suggests that *Cerastoderma edule* is susceptible to a range of pathogens and parasites. The effects of these may be exacerbated by stressors such as short immersion times and thermal stress (amongst others). As evidence exists for mass mortalities, resistance is assessed as ‘Low’ and resilience is assessed as ‘Medium’. Sensitivity is therefore categorised as ‘Medium’.

Removal of target species

Low

Q: High A: High C: High

Medium

Q: High A: High C: Medium

Medium

Q: High A: High C: Medium

The sedimentary biotope and characterizing and associated species may be disturbed and damaged by static or mobile gears that are targeting *Cerastoderma edule* or other species. These direct, physical impacts are assessed through the abrasion and penetration of the seabed pressures. The sensitivity assessment for this pressure considers any biological/ecological effects resulting from the removal of target species on this biotope. Dense populations of *Cerastoderma edule* on intertidal flats support commercial fisheries in several areas of the UK and the species is

also harvested throughout Europe. Harvesting may use mechanical methods (e.g. tractor dredges or hydraulic suction dredging) or hand collection using rakes or other methods. The fishery is managed through local bylaws and local target size classes are set (usually cockles below 20 mm are not collected). The commercial importance of the fishery has stimulated research on impacts on cockles and the sedimentary habitat and associated species. In some habitats removal of *Arenicola marina* and *Hediste diversicolor* for fishing bait may occur but these species are not considered to characterize this biotope and the removal of these as target species is not considered in this review; the relevant biotopes (LS.LSa.MuSa.LimAre; SS.SMu.IFiMu.Are; LS.LMu.MEst.HedMac), characterized by these species contain more information. The physical effects of harvesting on this species are addressed in the physical disturbance sections. Removal of *Cerastoderma edule* (cockles) by targeted harvesting may result in an altered community and may alter the character and reduce the spatial extent of the *Cerastoderma edule* and polychaetes in the littoral muddy sand biotope.

Coffen-Smout (1998) studied simulated fisheries impacts on *Cerastoderma edule* and reported that the cockle shell withstood between 12.9 and 171.4 newtons (N) of force depending on shell size and position of load (a 1 kg weight exerts about 10 N). Cockles are often damaged during mechanical harvesting, e.g. 5-15% were damaged by tractor dredging (Cotter *et al.*, 1997) and ca 20% were too damaged to be processed after hydraulic dredging (Pickett, 1973). Cook (1991) reported overall damage rates of 11-14% of rejects from rotary riddles on three hydraulic section dredgers operating. Undersized and rejected cockles may be stunned where these suffer prolonged vibrations from passage through mechanical gear and sorters, this can delay reburrowing, leading to increased predation and/or distribution by tidal waves and currents (Coffen-Smout & Rees, 1998).

Following size sorting (either mechanically or by hand), undersized cockles are deposited on the sediment surface. Damage rates and survival rates of harvested and discarded cockles and rates of reburrowing and displacement have been examined in a number of studies. The sediment on which discards are deposited affects burrowing. Experimental displacement to simulate harvesting impacts found that cockles deposited in pools are more able to rebury while none of those deposited on drained (and hence hard) sands were able to reburrow (Coffen-Smout & Rees, 1999). In this subtidal biotope, reburial rates should be high. Greater proportions of smaller cockles than medium or large reburrow, so that larger cockles are more likely to be displaced by tides (Coffen-Smout & Rees, 1999). Cockles that were transported up to 200m on the flood tide could reburrow if habitats in the new position were suitable (Coffen-Smout & Rees, 1999).

The method of harvesting cockles will influence the proportions that are removed and damaged. Pickett (1973) found that intense dredging for a short period on a bed of cockle spat had little effect on survival and growth although Cook (1991) found that impacts on small cockles from dredging were variable, with little reduction one year but a reduction in density observed the following year. Cotter *et al.* (1997) assessed the catch rates and damage and mortality of *Cerastoderma edule* resulting from experimental tractor dredging at the Burry Inlet (Wales). Stocks of adult cockles were reduced by 31 and 49% in low and high density areas respectively. Similarly mechanical cockle harvesting in muddy sand reduced the abundance of *Cerastoderma edule* by ca 34%. Populations had not recovered their original abundance after 174 days (Ferns *et al.*, 2000).

Hand raking for cockles on intertidal silty sandflats, using rakes that penetrated the surface by 5-10cm, resulted in a three-fold increase in the damage rate of cockles compared to control plots and, in the short-term, led to a relative decrease in the overall abundance of fauna (Kaiser *et al.*, 2001). After 56 days the small (9m²) plots had recovered but the larger (36m²) plots remained in an

altered state. Results collected over a year after the disturbance suggested that while effects of hand-raking may be significant within a year, they are unlikely to persist beyond this time-scale unless there are larger long-lived species present within the community (Kaiser et al. 2001).

The presence of dense cockle beds inhibit the establishment of other benthic species through space and resource competition, disturbance (Flach, 1996) and consumption of larvae (Andre et al., 2003). Removal of adult cockles by harvesting or other factors allows other species to establish. Following experimental removal of large adult *Cerastoderma edule* by Frid & Casear (2012) sediments showed increased biodiversity and assemblages dominated by traits common to opportunist taxa at a species-poor shore at Warton Sands, Morecambe Bay, and a more diverse shore at Thurstaston, Dee estuary. The movements of cockles disturb and exclude the amphipod *Corophium volutator* and other species (Flach, 1996; Flach & de Bruin, 1994) the removal of cockles may, therefore, allow this species to colonize intertidal flats. During periods of low cockle density, Desprez et al., (1992) observed that *Pygospio elegans* established dense populations; when cockles returned these were lost within one year.

It should be noted that removal of *Cerastoderma edule* by targeted harvesting may lead to wider ecological effects through starvation of shore birds in winter. This has been observed in the Dutch Wadden Sea (Smit et al., 1998). This effect is not directly of significance to this biotope and is not considered within the assessment.

Sensitivity assessment. Removal of the key characterizing species *Cerastoderma edule* by targeted harvesting would alter the character of the biotope and result in reclassification. The abundance of other soft-sediment infauna (particularly opportunist species such as *Pygospio elegans* and *Capitella capitata*) may increase in disturbed patches in the short-term as a result of the removal of cockles resulting in reduced competition for space and predation (on larvae). Where sediments remain suitable cockles are likely to recolonize via adult migration, survival of small, discarded cockles or via larval recruitment. In general fishing practices will be efficient at removing this species, resistance is therefore assessed as 'Low' (removal is not considered to be total as smaller individuals are not retained and harvesting is unlikely to be 100% efficient at removing larger cockles). Resilience is assessed as 'Medium' so that sensitivity is assessed as 'Medium'. Recovery will be influenced by a range of factors as outlined in the resilience section. Small patches are likely to be in-filled by adult cockle movement, large patches will recover through larval recruitment, which again is subject to many factors, and may be improved by the removal of adult cockles. However, as *Cerastoderma edule* recruitment is episodic, a recovery of 'Medium' to represent the recovery of age-classes from broad-scale removal was considered appropriate. Biotope sensitivity is therefore assessed as 'Medium'. Although some experiments have shown rapid recovery, the plots used in experiments are small and subject to low levels of harvesting compared to intertidal flats that are harvested at larger scales and where patches may be re-worked over a season.

Removal of non-target species

Low

Q: High A: High C: Medium

Medium

Q: High A: High C: Medium

Medium

Q: High A: High C: Medium

Dense beds of *Cerastoderma edule* occur in situations where the faunal assemblage is species-diverse and productive, but also where very few taxa are present (Cesar, 2012). These observations suggest that *Cerastoderma edule* populations are not dependent on other species and are therefore unlikely to be impacted by ecological/biological effects from the removal of others species. The removal of predators such as shrimp and crab may enhance recruitment of larvae (Beukema & Dekker, 2005). The physical effects of removal of other species such as polychaete

worms targeted by bait diggers may, however, impact *Cerastoderma edule* and other species associated with this biotope, through direct damage and removal and displacement. These direct effects of sediment disturbance are assessed in the physical damage sections.

The removal of *Cerastoderma edule* and other associated species would alter the biotope from the description and change community structure (diversity, biomass and abundance), potentially altering ecosystem function and the delivery of ecosystem goods and services (including the supply of food to fish and birds).

Sensitivity assessment. The assessment considers whether the removal of characterizing and associated species as by-catch would impact the biotope. Lethal damage to and removal of *Cerastoderma edule* and other species as by-catch would alter the character of the biotope. As *Cerastoderma edule* and *Limecola balthica* and other species are either sedentary or incapable of rapid evasive movements, resistance is assessed as 'Low'. Resilience is assessed as 'Medium' based on *Cerastoderma edule* and *Limecola balthica* and sensitivity is therefore categorized as 'Medium'. Physical damage to the sediment and other physical damage factors are considered in the abrasion and extraction pressures.

Bibliography

- André, C. & Lindegarth, M., 1995. Fertilization efficiency and gamete viability of a sessile, free-spawning bivalve, *Cerastoderma edule*. *Ophelia*, **43** (3), 215-227.
- André, C., Jonsson, P.R. & Lindegarth, M., 1993. Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. *Marine Ecology Progress Series*, **97**, 183-192.
- Ansell, A.D., Barnett, P.R.O., Bodoy, A. & Masse, H., 1981. Upper temperature tolerances of some European Mollusca III. *Cardium glaucum*, *C. tuberculata* and *C. edule*. *Marine Biology*, **65**, 177-183.
- Azevedo, C., 1997. Some observations on an amoeba, destructive agent of the gills of *Cerastoderma edule* (Mollusca, Bivalvia). *Diseases of Aquatic Organisms*, **30** (3), 223-225.
- Babarro, J.M. & de Zwaan, A., 2001. Factors involved in the (near) anoxic survival time of *Cerastoderma edule*: associated bacteria vs. endogenous fuel. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, **128** (3), 325-337.
- Ball, B., Munday, B. & Tuck, I., 2000b. Effects of otter trawling on the benthos and environment in muddy sediments. In: *Effects of fishing on non-target species and habitats*, (eds. Kaiser, M.J. & de Groot, S.J.), pp 69-82. Oxford: Blackwell Science.
- Bamber, R.N. & Spencer, J.F. 1984. The benthos of a coastal power station thermal discharge canal. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 603-623.
- Barber, B.J., 2004. Neoplastic diseases of commercially important marine bivalves. *Aquatic Living Resources*, **17** (04), 449-466.
- Bergman, M.J.N. & Hup, M., 1992. Direct effects of beam trawling on macro-fauna in a sandy sediment in the southern North Sea. *ICES Journal of Marine Science*, **49**, 5-11.
- Bergman, M.J.N. & Van Santbrink, J.W., 2000b. Fishing mortality of populations of megafauna in sandy sediments. In *The effects of fishing on non-target species and habitats* (ed. M.J. Kaiser & S.J. de Groot), 49-68. Oxford: Blackwell Science.
- Beukema, J., 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. *Journal of Experimental Marine Biology and Ecology*, **153** (1), 97-113.
- Beukema, J. & Cadée, G., 1999. An estimate of the sustainable rate of shell extraction from the Dutch Wadden Sea. *Journal of Applied Ecology*, **36** (1), 49-58.
- Beukema, J. & De Vlas, J., 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Marine Ecology Progress Series*. Oldendorf, **52** (2), 193-200.
- Beukema, J. & Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. *Marine Ecology Progress Series*, **287**, 149-167.
- Beukema, J., Essink, K., Michaelis, H. & Zwarts, L., 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? *Netherlands Journal of Sea Research*, **31** (4), 319-330.
- Beukema, J.J., 1979. Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. *Netherlands Journal of Sea Research*, **13**, 203-223.
- Beukema, J.J., 1985. Growth and dynamics in populations of *Echinocardium cordatum* living in the North Sea off the Dutch coast. *Netherlands Journal of Sea Research*, **19**, 129-134.
- Beukema, J.J., 1990. Expected effects of changes in winter temperatures on benthic animals living in soft sediments in coastal North Sea areas. In *Expected effects of climatic change on marine coastal ecosystems* (ed. J.J. Beukema, W.J. Wolff & J.J.W.M. Brouns), pp. 83-92. Dordrecht: Kluwer Academic Publ.
- Bolam, S., Whomersley, P. & Schratzberger, M., 2004. Macrofaunal recolonization on intertidal mudflats: effect of sediment organic and sand content. *Journal of Experimental Marine Biology and Ecology*, **306** (2), 157-180.
- Bolam, S.G., 1999. *An Investigation Into The Processes Responsible For The Generation Of The Spatial Pattern Of The Spionid Polychaete Pygospio Elegans Claparede*. Napier University.
- Bonsdorff, E., 1984. Establishment, growth and dynamics of a *Macoma balthica* (L.) population. *Limnologica* (Berlin), **15**, 403-405.
- Borja, A., Franco, J. & Perez, V., 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin*, **40** (12), 1100-1114.
- Bouchet, V.M. & Sauriau, P.-G., 2008. Influence of oyster culture practices and environmental conditions on the ecological status of intertidal mudflats in the Pertuis Charentais (SW France): A multi-index approach. *Marine Pollution Bulletin*, **56** (11), 1898-1912.
- Bouma, H., Duiker, J., De Vries, P., Herman, P. & Wolff, W., 2001. Spatial pattern of early recruitment of *Macoma balthica* (L.) and *Cerastoderma edule* (L.) in relation to sediment dynamics on a highly dynamic intertidal sandflat. *Journal of Sea Research*, **45** (2), 79-93.
- Boyden, C., 1971. A comparative study of the reproductive cycles of the cockles *Cerastoderma edule* and *C. glaucum*. *Journal of the Marine Biological Association of the United Kingdom*, **51** (03), 605-622.
- Boyden, C.R. & Russel, P.J.C., 1972. The distribution and habitat range of the brackish water cockle (*Cardium* (*Cerastoderma*) *edule*) in the British Isles. *Journal of Animal Ecology*, **41**, 719-734.
- Brafield, A.E. & Newell, G.E., 1961. The behaviour of *Macoma balthica* (L.). *Journal of the Marine Biological Association of the United Kingdom*, **41**, 81-87.

- Brafield, A.E., 1963. The effects of oxygen deficiency on the behaviour of *Macoma balthica*. *Animal Behaviour*, **11**, 245-346.
- Brenchley, G.A., 1981. Disturbance and community structure : an experimental study of bioturbation in marine soft-bottom environments. *Journal of Marine Research*, **39**, 767-790.
- Bridges, T.S., Levin, L.A., Cabrera, D. & Plaia, G., 1994. Effects of sediment amended with sewage, algae, or hydrocarbons on growth and reproduction in two opportunistic polychaetes. *Journal of Experimental Marine Biology and Ecology*, **177** (1), 99-119.
- Brock, V., 1979. Habitat selection of two congeneric bivalves, *Cardium edule* and *C. glaucum* in sympatric and allopatric populations. *Marine Biology*, **54**, 149-156.
- Bryan, G.W. & Gibbs, P.E., 1983. *Heavy metals from the Fal estuary, Cornwall: a study of long-term contamination by mining waste and its effects on estuarine organisms*. Plymouth: Marine Biological Association of the United Kingdom. [Occasional Publication, no. 2.]
- Burdon, D., Callaway, R., Elliott, M., Smith, T. & Wither, A., 2014. Mass mortalities in bivalve populations: A review of the edible cockle *Cerastoderma edule* (L.). *Estuarine, Coastal and Shelf Science*, **150**, 271-280.
- Caddy, J.F., 1967. Maturation of gametes and spawning in *Macoma balthica* (L.). *Canadian Journal of Zoology*, **45**, 955-965.
- Castel, J., Labourg, P.-J., Escaravage, V., Auby, I. & Garcia, M.E., 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio-and macrobenthos in tidal flats. *Estuarine, Coastal and Shelf Science*, **28** (1), 71-85.
- Cesar, C.P. & Frid, C.L., 2012. Benthic disturbance affects intertidal food web dynamics: implications for investigations of ecosystem functioning. *Marine Ecology Progress Series*, **466**, 35.
- Chandrasekara, W.U. & Frid, C.L.J., 1998. A laboratory assessment of the survival and vertical movement of two epibenthic gastropod species, *Hydrobia ulvae*, (Pennant) and *Littorina littorea* (Linnaeus), after burial in sediment. *Journal of Experimental Marine Biology and Ecology*, **221**, 191-207.
- Clay, E., 1967b. Literature survey of the common fauna of estuaries, 10. *Macoma balthica* and *Tellina tenuis*. *Imperial Chemical Industries Limited, Brixham Laboratory, BL/A/705*.
- Coffen-Smout, S., 1998. Shell strength in the cockle *Cerastoderma edule* L. under simulated fishing impacts. *Fisheries Research*, **38** (2), 187-191.
- Coffen-Smout, S.S. & Rees, E.I.S., 1999. Burrowing behaviour and dispersion of cockles *Cerastoderma edule* following simulated fishing disturbance. *Fisheries Research*, **40**, 65-72.
- Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B., 2004. The Marine Habitat Classification for Britain and Ireland. Version 04.05. ISBN 1 861 07561 8. In JNCC (2015), *The Marine Habitat Classification for Britain and Ireland Version 15.03*. [2019-07-24]. Joint Nature Conservation Committee, Peterborough. Available from <https://mhc.jncc.gov.uk/>
- Cook, W., 1991. *Studies on the effects of hydraulic dredging on cockle and other macroinvertebrate populations 1989-1990*. LANCASTER UNIV., LANCASTER(UK). 1991.
- Coscia, I., Robins, P.E., Porter, J.S., Malham, S.K. & Ironside, J.E., 2013. Modelled larval dispersal and measured gene flow: seascape genetics of the common cockle *Cerastoderma edule* in the southern Irish Sea. *Conservation Genetics*, **14** (2), 451-466.
- Cotter, A.J.R., Walker, P., Coates, P., Cook, W. & Dare, P.J., 1997. Trial of a tractor dredger for cockles in Burry Inlet, South Wales. *ICES Journal of Marine Science*, **54**, 72-83.
- Crisp, D.J. (ed.), 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, **33**, 165-210.
- Dare, P. & Walker, P., 1993. Spatfalls of cockles and mussels in the Wash in relation to preceding winter temperatures and possible effects of spring wind regimes upon larval dispersal: a preliminary analysis. Second Yerseke Workshop, Yerseke.
- De Montaudouin, X., 1997. Potential of bivalves' secondary settlement differs with species: a comparison between cockle (*Cerastoderma edule*) and clam (*Ruditapes philippinarum*) juvenile resuspension. *Marine Biology*, **128** (4), 639-648.
- de Wilde, P.A.W., 1975. Influence of temperature on behaviour, energy metabolism and growth of *Macoma balthica* (L.). In *Ninth European Marine Biology Symposium* (ed. H. Barnes), pp.239-256. Aberdeen University Press.
- de Zwaan, A., Babarro, J.M., Monari, M. & Cattani, O., 2002. Anoxic survival potential of bivalves:(arte) facts. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **131** (3), 615-624.
- Degraer, S., Wittoeck, J., Appeltans, W., Cooreman, K., Deprez, T., Hillewaert, H., Hostens, K., Mees, J., Berge, V. & Vincx, M., 2006. *The macrobenthos atlas of the Belgian part of the North Sea*. Belgian Science Policy.
- Dernie, K.M., Kaiser, M.J., Richardson, E.A. & Warwick, R.M., 2003. Recovery of soft sediment communities and habitats following physical disturbance. *Journal of Experimental Marine Biology and Ecology*, **285-286**, 415-434.
- Deslous-Paoli, J.-M., Lannou, A.-M., Geairon, P., Bougrier, S., Raillard, O. & Héral, M., 1992. Effects of the feeding behavior of *Crassostrea gigas* (Bivalve Molluscs) on biosedimentation of natural particulate matter. *Hydrobiologia*, **231** (2), 85-91.
- Desprez, M.H., Rybarczyk, H., Wilson, J.G., Ducrotoy, J.P., Sueur, F., Olivesi, R. & Elkaim, B., 1992. Biological impact of eutrophication in the Bay of Somme and the induction and impact of anoxia. *Netherlands Journal of Sea Research*, **30**, 149-159.
- Dries, R.R. & Theede, H., 1974. Sauerstoffmangelresistenz mariner Bodenvertebraten aus der West-lichen Ostsee. *Marine Biology*, **25**, 327-233.
- Ducrotoy, C.R., Rybarczyk, H., Souprayan, J., Bachelet, G., Beukema, J.J., Desprez, M., Dörjes, J., Essink, K., Guillou, J., Michaelis, H., Sylvand, B., Wilson, J.G., Elkaïm, B. & Ibanez, F., 1991. A comparison of the population dynamics of the cockle (*Cerastoderma edule*) in North-Western Europe. In *Proceedings of the Estuarine and Coastal Sciences Association Symposium, ECSA 19, 4-8 September 1989*,

- University of Caen, France. *Estuaries and Coasts: Spatial and Temporal Intercomparisons*, pp. 173-184. Denmark: Olsen & Olsen.
- Elliot, M., Nedwell, S., Jones, N.V., Read, S.J., Cutts, N.D. & Hemingway, K.L., 1998. Intertidal sand and mudflats & subtidal mobile sandbanks (Vol. II). An overview of dynamic and sensitivity for conservation management of marine SACs. *Prepared by the Scottish Association for Marine Science for the UK Marine SACs Project*.
- Emerson, C.W. & Grant, J., 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnology and Oceanography*, **36**, 1288-1300.
- Fenchel, T.M. & Reidl, R.J., 1970. The sulphide system: a new biotic community underneath the oxidised layer of marine sand bottoms. *Marine Biology*, **7**, 255-268.
- Ferns, P.N., Rostron, D.M. & Siman, H.Y., 2000. Effects of mechanical cockle harvesting on intertidal communities. *Journal of Applied Ecology*, **37**, 464-474.
- Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore*. Cambridge: Cambridge University Press.
- Flach, E.C. & De Bruin, W., 1994. Does the activity of cockles, *Cerastoderma edule* (L.) and lugworms, *Arenicola marina* (L.), make *Corophium volutator* Pallas more vulnerable to epibenthic predators: a case of interaction modification? *Journal of Experimental Marine Biology and Ecology*, **182**, 265-285.
- Flach, E.C., 1996. The influence of the cockle, *Cerastoderma edule*, on the macrozoobenthic community of tidal flats of the Wadden Sea. *Marine Biology*, **17**, 87-98.
- Folk, R.L., 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. **62**, *The Journal of Geology*, 344-359.
- Franklin, A. & Pickett, G.D., 1978. Studies of the indirect effects of fishing on stocks of cockles, *Cardium edule*, in the Thames estuary and Wash. *Fisheries Research, Technical Report*, no. 42, MAFF, Lowestoft, pp. 9.
- Gam, M., de Montaudouin, X. & Bazairi, H., 2010. Population dynamics and secondary production of the cockle *Cerastoderma edule*: a comparison between Merja Zerga (Moroccan Atlantic Coast) and Arcachon Bay (French Atlantic Coast). *Journal of Sea Research*, **63** (3), 191-201.
- Genelt-Yanovskiy, E., Poloskin, A., Granovitch, A., Nazarova, S. & Strelkov, P., 2010. Population structure and growth rates at biogeographic extremes: a case study of the common cockle, *Cerastoderma edule* (L.) in the Barents Sea. *Marine Pollution Bulletin*, **61** (4), 247-253.
- Gibbs, P.E., 1968. Observations on the population of *Scoloplos armiger* at Whitstable. *Journal of the Marine Biological Association of the United Kingdom*, **48**, 225-254.
- Gilbert, M.A., 1978. Aspects of the reproductive cycle in *Macoma balthica* (Bivalvia). *The Nautilus*, **29**, 21-24.
- Gittenberger, A. & Van Loon, W.M.G.M., 2011. Common Marine Macrozoobenthos Species in the Netherlands, their Characteristics and Sensitivities to Environmental Pressures. GiMaRIS report no 2011.08. DOI: [10.13140/RG.2.1.3135.7521](https://doi.org/10.13140/RG.2.1.3135.7521)
- Gorbushin, A.M., Levakin, I.A., Panchina, N.A. & Panchin, Y.V., 2001. *Hydrobia ulvae* (Gastropoda: Prosobranchia): a new model for regeneration studies. *Journal of Experimental Biology*, **204** (2), 283-289.
- Grant, J. & Thorpe, B., 1991. Effects of suspended sediment on growth, respiration, and excretion of the soft shelled clam (*Mya arenaria*). *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1285-1292.
- Grassle, J.F. & Grassle, J.P., 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *Journal of Marine Research*, **32**, 253-284.
- Grave, S.D., Moore, S.J. & Burnell, G., 1998. Changes in benthic macrofauna associated with intertidal oyster, *Crassostrea gigas* (Thunberg) culture. *Journal of Shellfish Research*, **17** (4), 1137-1142.
- Gray, J.S., 1979. Pollution-induced changes in populations. *Philosophical Transactions of the Royal Society of London, Series B*, **286**, 545-561.
- Gray, J.S., 1981. *The ecology of marine sediments. An introduction to the structure and function of benthic communities*. Cambridge: Cambridge University Press.
- Green, J., 1968. *The biology of estuarine animals*. Sidgwick and Jackson, London.
- Gubbay, S., & Knapman, P.A., 1999. *A review of the effects of fishing within UK European marine sites*. Peterborough, English Nature.
- Guenther, C.P., 1991. Settlement of *Macoma balthica* on an intertidal sandflat in the Wadden Sea. *Marine Ecology Progress Series*, **76**, 73-79.
- Guillou, J. & Tartu, C., 1994. Post-larval and juvenile mortality in a population of the edible cockle *Cerastoderma edule* (L.) from Northern Brittany. *Netherlands Journal of Sea Research*, **33**, 103-111.
- Hall, J.A. & Frid, C.L.J., 1995. Response of estuarine benthic macrofauna in copper-contaminated sediments to remediation of sediment quality. *Marine Pollution Bulletin*, **30**, 694-700.
- Hall, K., Paramour, O.A.L., Robinson, L.A., Winrow-Giffin, A., Frid, C.L.J., Eno, N.C., Dernie, K.M., Sharp, R.A.M., Wyn, G.C. & Ramsay, K., 2008. Mapping the sensitivity of benthic habitats to fishing in Welsh waters - development of a protocol. *CCW (Policy Research) Report No: 8/12, Countryside Council for Wales (CCW), Bangor*, 85 pp.
- Hall, S.J. & Harding, M.J.C., 1997. Physical disturbance and marine benthic communities: the effects of mechanical harvesting of cockles on non-target benthic infauna. *Journal of Applied Ecology*, **34**, 497-517.
- Hancock, D.A. & Urquhart, A.E., 1964. Mortalities of edible cockles (*Cardium edule* L.) during the severe winter of 1962-64. *Journal*

of the Marine Biological Association of the United Kingdom, **33**, 176-178.

Harvey, M. & Vincent, B., 1989. Spatial and temporal variations of the reproduction cycle and energy allocation of the bivalve *Macoma balthica* (L.) on a tidal flat. *Journal of Experimental Marine Biology and Ecology*, **129**, 199-217.

Herrando-Perez, S. & Frid, C.L.J., 2001. Recovery patterns of macrobenthos and sediment at a closed fly-ash dumpsite. *Sarsia*, **86** (4-5), 389-400.

Hiddink, J. & Wolff, W., 2002. Changes in distribution and decrease in numbers during migration of the bivalve *Macoma balthica*. *Marine Ecology Progress Series*. **233**, 117-130

Hiddink, J.G., 2003. Effects of suction-dredging for cockles on non-target fauna in the Wadden Sea. *Journal of Sea Research*, **50**, 315-323.

Hiscock, K., Sewell, J. & Oakley, J., 2005. *Marine Health Check 2005. A report to gauge the health of the UK's sea-life*. Godalming, WWF-UK.

Hiscock, K., Tyler-Walters, H. & Jones, H., 2002. High level environmental screening study for offshore wind farm developments - marine habitats and species project. *Marine Biological Association of the United Kingdom*, Plymouth, AEA Technology, Environment Contract: W/35/00632/00/00, pp.

Honkoop, P. & Van der Meer, J., 1998. Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **220** (2), 227-246.

Hornberger, M.I., Luoma, S.N., Cain, D.J., Parchaso, F., Brown, C.L., Bouse, R.M., Wellise, C. & Thompson, J.K., 2000. Linkage of bioaccumulation and biological effects to changes in pollutant loads in South San Francisco Bay. *Environmental science & technology*, **34** (12), 2401-2409.

Humphreys, J., Caldow, R.W., McGrorty, S., West, A.D. & Jensen, A.C., 2007. Population dynamics of naturalised Manila clams *Ruditapes philippinarum* in British coastal waters. *Marine Biology*, **151** (6), 2255-2270.

Huthnance, J., 2010. Ocean Processes Feeder Report. London, *DEFRA on behalf of the United Kingdom Marine Monitoring and Assessment Strategy (UKMMAS) Community*.

Huxham, M. & Richards, M., 2003. Can postlarval bivalves select sediment type during settlement? A field test with *Macoma balthica* (L.) and *Cerastoderma edule* (L.). *Journal of Experimental Marine Biology and Ecology*, **288** (2), 279-293.

Iglesias, J., Urrutia, M., Navarro, E., Alvarez-Jorna, P., Larretxea, X., Bougrier, S. & Heral, M., 1996. Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition. *Journal of Experimental Marine Biology and Ecology*, **197** (1), 121-143.

Jackson, M.J. & James, R., 1979. The influence of bait digging on cockle *Cerastoderma edule*, populations in north Norfolk. *Journal of Applied Ecology*, **16**, 671-679.

Jensen, K.T., 1992. Macrozoobenthos on an intertidal mudflat in the Danish Wadden Sea: Comparisons of surveys made in the 1930s, 1940s and 1980s. *Helgolander Meeresuntersuchungen*. Hamburg, **46** (4), 363-376.

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

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

Jonssen, P.R. & Andre, C., 1992. Mass mortality of the bivalve *Cerastoderma edule* on the Swedish west coast caused by infestation with the digenean trematode *Cercaria cerastodermæ* I. *Ophelia*, **36**, 151-157.

Kaiser, M. & Beadman, H., 2002. Scoping study of the carrying capacity for bivalve cultivation in the coastal waters of Great Britain. *The Crown Estate. Interim Report*.

Kaiser, M.J., Ramsay, K. & Hughes, R.N., 1998. Can fisheries influence interspecific competition in sympatric populations of hermit crabs? *Journal of Natural History*, **32**, 521-531.

Kamermans, P., 1993. Food limitation in cockles (*Cerastoderma edule* (L.)): influences of location on tidal flat and of nearby presence of mussel beds. *Netherlands Journal of Sea Research*, **31** (1), 71-81.

Kingston, P., 1974. Some observations on the effects of temperature and salinity upon the growth of *Cardium edule* and *Cardium glaucum* larvae in the laboratory. *Journal of the Marine Biological Association of the United Kingdom*, **54**, 309-317.

Kraan, C., Piersma, T., Dekinga, A., Koolhaas, A. & Van der Meer, J., 2007. Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna. *ICES Journal of Marine Science: Journal du Conseil*, **64** (9), 1735-1742.

Kristensen, I., 1958. Differences in density and growth in a cockle population in the Dutch Wadden Sea. *Archives Néerlandaises de Zoologie*, **12**, 351-453.

Kruse, I. & Reise, K., 2003. Reproductive isolation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae) indicates sibling species in the North Sea. *Marine Biology*, **143** (3), 511-517.

Kruse, I., Strasser, M. & Thiermann, F., 2004. The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae). *Journal of Sea Research*, **51**, 53-62.

Langston, W.J., Chesman, B.S., Burt, G.R., Hawkins, S.J., Readman, J. & Worsfold, P., 2003. Characterisation of European Marine Sites. Poole Harbour Special Protection Area. *Occasional Publication. Marine Biological Association of the United Kingdom*, **12**, 111.

- Leppäkoski, E., 1975. Assessment of degree of pollution on the basis of macrozoobenthos in marine and brackish water environments. *Acta Academiae Åboensis, Series B*, **35**, 1-90.
- Levell, D., Rostron, D. & Dixon, I.M.T., 1989. Sediment macrobenthic communities from oil ports to offshore oilfields. In *Ecological Impacts of the Oil Industry*, Ed. B. Dicks. Chichester: John Wiley & Sons Ltd.
- Lin, J. & Hines, A.H., 1994. Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, *Macoma balthica*. *Oikos*, **69**, 28-36.
- Lindsay, S.M., Jackson, J.L. & He, S.Q., 2007. Anterior regeneration in the spionid polychaetes *Dipolydora quadrilobata* and *Pygospio elegans*. *Marine Biology*, **150** (6), 1161-1172.
- Long, D., 2006. BGS detailed explanation of seabed sediment modified Folk classification. Available from: http://www.emodnet-seabedhabitats.eu/PDF/GMHM3_Detailed_explanation_of_seabed_sediment_classification.pdf
- Longshaw, M. & Malham, S.K., 2013. A review of the infectious agents, parasites, pathogens and commensals of European cockles (*Cerastoderma edule* and *C. glaucum*). *Journal of the Marine Biological Association of the United Kingdom*, **93** (01), 227-247.
- Mathalon, A. & Hill, P., 2014. Microplastic fibers in the intertidal ecosystem surrounding Halifax Harbor, Nova Scotia. *Marine Pollution Bulletin*, **81** (1), 69-79.
- Maurer, D., Keck, R.T., Tinsman, J.C., Leatham, W.A., Wethe, C., Lord, C. & Church, T.M., 1986. Vertical migration and mortality of marine benthos in dredged material: a synthesis. *Internationale Revue der Gesamten Hydrobiologie*, **71**, 49-63.
- McCall, P.L., 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *Journal of Marine Research*, **35**, 221-266.
- McLaughlin, E., Portig, A. & Johnson, M.P., 2007. Can traditional harvesting methods for cockles be accommodated in a Special Area of Conservation? *ICES Journal of Marine Science: Journal du Conseil*, **64** (2), 309-317.
- McLusky, D.S. & Allan, D.G., 1976. Aspects of the biology of *Macoma balthica* (L.) from the estuarine Firth of Forth. *Journal of Molluscan Studies*, **42**, 31-45.
- McLusky, D.S., 1982. The impact of petrochemical effluent on the fauna of an intertidal estuarine mudflat. *Estuarine, Coastal and Shelf Science*, **14**, 489-499.
- MES, 2010. *Marine Macrofauna Genus Trait Handbook*. Marine Ecological Surveys Limited. <http://www.genustraithandbook.org.uk/>
- Mitchell, I.M., 2006. In situ biodeposition rates of Pacific oysters (*Crassostrea gigas*) on a marine farm in Southern Tasmania (Australia). *Aquaculture*, **257** (1), 194-203.
- Montaudouin de X. & Bachelet, G., 1996. Experimental evidence of complex interactions between biotic and abiotic factors in the dynamics of an intertidal population of the bivalve *Cerastoderma edule*. *Oceanologica Acta*, **19**, 449-463.
- Moore, J., 1991. Studies on the Impact of Hydraulic Cockle Dredging on Intertidal Sediment Flat Communities. A report to the Nature Conservancy Council from the Field Studies Council Research Centre, Pembroke, Wales, FSC/RC/4/91.
- Morton, B., 2008. The evolution of eyes in the Bivalvia: New Insights*. *American Malacological Bulletin*, **26** (1/2), 35-45.
- Navarro, E., Iglesias, J.I.P. & Ortega, M.M., 1992. Natural sediment as a food source for the cockle *Cerastoderma edule* (L.), effects of variable particle concentrations on feeding, digestion and scope for growth. *Journal of Experimental Marine Biology and Ecology*, **156**, 69-87.
- Navarro, J.M. & Widdows, J., 1997. Feeding physiology of *Cerastoderma edule* in response to a wide range of seston concentrations. *Marine Ecology Progress Series*, **152**, 175-186.
- Newell, R.I.E. & Bayne, B.L., 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium (=Cerastoderma) edule* (Bivalvia: Cardidae). *Marine Biology*, **56**, 11-19.
- Nugues, M., Kaiser, M., Spencer, B. & Edwards, D., 1996. Benthic community changes associated with intertidal oyster cultivation. *Aquaculture Research*, **27** (12), 913-924.
- Oertzen, J.A. Von., 1969. Erste Ergebnisse zur experimentellen ökologie von postglazialen Relikten (Bivalvia) der Ostsee. *Limnologica (Berlin)*, **7**, 129-137.
- Olafsson, E.B., 1989. Contrasting influences of suspension-feeding and deposit-feeding populations of *Macoma balthica* on infaunal recruitment. *Marine Ecology Progress Series*. Oldendorf, **55** (2), 171-179.
- Olivier, M., Desrosiers, G. & Vincent, B., 1992. Variations in growth and mortality of juveniles of the phyllodocid *Eteone longa* (Fabricius) on a tidal flat. *Canadian Journal of Zoology*, **70** (4), 663-669.
- OSPAR Commission. 2009. Background document for *Modiolus modiolus* beds. *OSPAR Commission Biodiversity Series*. OSPAR Commission: London. Available from: <http://www.ospar.org/documents?v=7193>
- Pearson, T.H. & Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review*, **16**, 229-311.
- Pedersen, T.F., 1991. Metabolic adaptations to hypoxia of two species of Polychaeta, *Nephtys ciliata* and *Nephtys hombergii*. *Journal of Comparative Physiology B*, **161** (2), 213-215.
- Peterson, C.H. & Black, R., 1987. Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. *Limnology and Oceanography*, **32** (1), 143-166.
- Peterson, C.H. & Black, R., 1991. Preliminary evidence for progressive sestonic food depletion in incoming tide over a broad tidal sand flat. *Estuarine, Coastal and Shelf Science*, **32** (4), 405-413.

- Peterson, C.H. & Skilleter, G.A., 1994. Control of foraging behaviour of individuals within an ecosystem context: The clam *Macoma balthica*, flow environment and siphon-cropping fishes. *Oecologia*, **100**, 256-267.
- Philippart, C.J., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C. & Dekker, R., 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography*, **48** (6), 2171-2185.
- Pickett, G.D., 1973. The impact of mechanised harvesting on the Thames estuary cockle fishery. *MAFF Laboratory Leaflet*, no. 29, Fisheries Laboratory, Lowestoft, pp. 9.
- Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R. & Essink, K., 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology*, **38** (5), 976-990.
- Purschke, G., Arendt, D., Hausen, H. & Müller, M.C., 2006. Photoreceptor cells and eyes in *Annelida*. *Arthropod Structure & Development*, (4), 211-230.
- Ragnarsson, S.Á. & Raffaelli, D., 1999. Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments. *Journal of Experimental Marine Biology and Ecology*, **241** (1), 31-43.
- Rasmussen, E., 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia*, **11**, 1-507.
- Ratcliffe, P.J., Jones, N.V. & Walters, N.J., 1981. The survival of *Macoma balthica* (L.) in mobile sediments. In *Feeding and survival strategies of estuarine organisms* (ed. N.V. Jones and W.J. Wolff), pp. 91-108. Plenum Press.
- Reise, K., 1979. Spatial configurations generated by motile benthic polychaetes. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **32**, 55-72.
- Rhoads, D.C. & Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research*, **28**, 150-178.
- Richardson, C.A., Ibarrola, I. & Ingham, R.J., 1993b. Emergence pattern and spatial distribution of the common cockle *Cerastoderma edule*. *Marine Ecology Progress Series*, **99**, 71-81.
- Rosenberg, R. & Loo, L., 1988. Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia*, **29**, 213-225.
- Rosenberg, R., Hellman, B. & Johansson, B., 1991. Hypoxic tolerance of marine benthic fauna. *Marine Ecology Progress Series*, **79**, 127-131.
- Rossi, F., Forster, R., Montserrat, F., Ponti, M., Terlizzi, A., Ysebaert, T. & Middelburg, J., 2007. Human trampling as short-term disturbance on intertidal mudflats: effects on macrofauna biodiversity and population dynamics of bivalves. *Marine Biology*, **151** (6), 2077-2090.
- Rostron, D.M., 1998. *Sea Empress* oil spill: sediment shore impact assessment. Infauna of heavily oiled shores at Milford Haven and Carmarthen Bay. *CCW Sea Empress Contract Report*, no. 144, 49 pp.
- Russell, P.J.C. & Petersen, G.H., 1973. The use of ecological data in the elucidation of some shallow water European *Cardium* species. *Malacologia*, **14**, 223-232.
- Rygg, B., 1970. Studies on *Cerastoderma edule* (L.) and *Cerastoderma glaucum* (Poiret). *Sarsia*, **43**, 65-80.
- Rygg, B., 1985. Effect of sediment copper on benthic fauna. *Marine Ecology Progress Series*, **25**, 83-89.
- Samuelson, G.M., 2001. Polychaetes as indicators of environmental disturbance on subarctic tidal flats, Iqaluit, Baffin Island, Nunavut Territory. *Marine Pollution Bulletin*, **42** (9), 733-741.
- Sanchez-Salazar, M.E., Griffiths, C.C. & Seed, R., 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule*. *Estuarine, Coastal and Shelf Science*, **25**, 245-260.
- Sanders, H.L., 1968. Marine Benthic Diversity: A Comparative Study. *The American Naturalist*, **102** (925), 243.
- Savari, A., Lockwood, A.P.M. & Shearer, M., 1991a. Variation in the physiological state of the common cockle (*Cerastoderma edule* (L.)) in the laboratory and in Southampton Water. *Journal of Molluscan Studies*, **57**, 33-34.
- Savari, A., Lockwood, A.P.M. & Shearer, M., 1991b. Effects of season and size (age) on heavy metal concentration of the common cockle (*Cerastoderma edule* (L.)) from Southampton Water. *Journal of Molluscan Studies*, **57**, 33-44.
- Schöttler, U., 1982. An investigation on the anaerobic metabolism of *Nephtys hombergii* (Annelida: Polychaeta). *Marine Biology*, **71** (3), 265-269.
- Schuitema, K. A., 1970. Verspreiding en verplaatsing van *Cardium edule* L. binnen een populatie. *NIOZ-Report*, **7**; 45 pp.
- Shaw, D.G., Paul, A.J., Cheek, L.M. & Feder, H.M., 1976. *Macoma balthica*: An indicator of oil pollution. *Marine Pollution Bulletin*, **7**, 29-31.
- Sheehan, E.V., 2007. *Ecological impact of the Carcinus maenas (L.) fishery 'crab-tiling' on estuarine fauna*. Ph.D. thesis, University of Plymouth.
- Simenstad, C.A. & Fresh, K.L., 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: scales of disturbance. *Estuaries*, **18** (1), 43-70.
- Smaal, A., van Stralen, M. & Craeymeersch, J., 2005. Does the introduction of the Pacific oyster *Crassostrea gigas* lead to species shifts in the Wadden Sea? The comparative roles of suspension-feeders in ecosystems: *Springer*, **47**, 277-289.
- Smaal, A.C., Vonck, A.P.M.A. & Bakker, M., 1997. Seasonal variation in physiological energetics of *Mytilus edulis* and *Cerastoderma edule* of different size classes. *Journal of the Marine Biological Association of the United Kingdom*, **77**, 817-838.

- Smit, C.J., Dankers, N., Ens, B.J. & Meijboom, A., 1998. Birds, mussels, cockles and shellfish fishery in the Dutch Wadden Sea: How to deal with low food stocks for eiders and oystercatchers? *Senckenbergiana Maritima*, **29** (1-6), 141-153.
- Sörlin, T., 1988. Floating behaviour in the tellinid bivalve *Macoma balthica* (L.). *Oecologia*, **77**, 273-277.
- Sornin, J.-M., Feuillet, M., Heral, M. & Deslous-Paoli, J.-M., 1983. Effet des biodépôts de l'huître *Crassostrea gigas* (Thunberg) sur l'accumulation de matières organiques dans les parcs du bassin de Marennes-Oléron. *Journal of Molluscan Studies*, **49** (supp12A), 185-197.
- Stekoll, M.S., Clement, L.E. & Shaw, D.G., 1980. Sublethal effects of chronic oil exposure on the intertidal clam *Macoma balthica*. *Marine Biology*, **57**, 51-60.
- Strasser, M. & Günther, C-P., 2001. Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. *Journal of Sea Research*, **46**, 57-67.
- Tebble, N., 1976. *British Bivalve Seashells. A Handbook for Identification*, 2nd ed. Edinburgh: British Museum (Natural History), Her Majesty's Stationary Office.
- Tenore, K.R., 1977. Growth of *Capitella capitata* cultured on various levels of detritus derived from different sources. *Limnology and Oceanography*, **22** (5), 936-941.
- Tenore, K.R. & Chesney, E.J., 1985. The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete, *Capitella capitata* (type 1). *Limnology and Oceanography*, **30** (6), 1188-1195.
- Theede, H., 1984. Physiological approaches to environmental problems of the Baltic. *Limnologica (Berlin)*, **15**, 443-458.
- Theede, H., Ponat, A., Hiroki, K. & Schlieper, C., 1969. Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Marine Biology*, **2**, 325-337.
- Thiel, M., Stearns, L. & Watling, L., 1998. Effects of green algal mats on bivalves in a New England mud flat. *Helgoländer Meeresuntersuchungen*, **52** (1), 15-28.
- Thieltges, D.W., 2006. Parasite induced summer mortality in the cockle *Cerastoderma edule* by the trematode *Gymnophallus choledochus*. *Hydrobiologia*, **559** (1), 455-461.
- Tillin, H.M., Hull, S.C. & Tyler-Walters, H., 2010. Development of a sensitivity matrix (pressures-MCZ/MPA features). *Report to the Department of the Environment, Food and Rural Affairs from ABPmer, Southampton and the Marine Life Information Network (MarLIN) Plymouth: Marine Biological Association of the UK., Defra Contract no. MB0102 Task 3A, Report no. 22., London, 145 pp.*
- Troost, K., Stamhuis, E.J., van Duren, L.A. & Wolff, W.J., 2009. Feeding current characteristics of three morphologically different bivalve suspension feeders, *Crassostrea gigas*, *Mytilus edulis* and *Cerastoderma edule*, in relation to food competition. *Marine Biology*, **156** (3), 355-372.
- Trueman, E.R. & Ansell, A.D., 1969. The mechanisms of burrowing into soft substrata by marine animals. *Oceanography and Marine Biology: an Annual Review*, **7**, 315-366.
- Turk, T.R. & Risk, M.J., 1981. Invertebrate populations of Cobequid Bay, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 642-648.
- Tyler-Walters, H., 2007. *Cerastoderma edule* Common cockle. 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. Available from: <http://www.marlin.ac.uk/species/detail/1384>
- Tyler-Walters, H. & Arnold, C., 2008. Sensitivity of Intertidal Benthic Habitats to Impacts Caused by Access to Fishing Grounds. *Report to Cyngor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN) [Contract no. FC 73-03-327]*, Marine Biological Association of the UK, Plymouth, 48 pp. Available from: www.marlin.ac.uk/publications
- UKTAG, 2014. UK Technical Advisory Group on the Water Framework Directive [online]. Available from: <http://www.wfduk.org>
- Van Colen, C., Montserrat, F., Vincx, M., Herman, P.M., Ysebaert, T. & Degraer, S., 2008. Macrobenthic recovery from hypoxia in an estuarine tidal mudflat. *Marine Ecology-Progress Series*, **372**, 31-42.
- Van Hoey, G., Degraer, S. & Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science*, **59** (4), 599-613.
- Villalba, A., Iglesias, D., Ramilo, A., Darriba, S., Parada, J.M., No, E., Abollo, E., Molares, J. & Carballal, M.J., 2014. Cockle *Cerastoderma edule* fishery collapse in the Ria de Arousa (Galicia, NW Spain) associated with the protistan parasite *Marteilia cochillia*. *Diseases of Aquatic Organisms*, **109** (1), 55-80.
- Warren, L.M., 1977. The ecology of *Capitella capitata* in British waters. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 151-159.
- Wegeberg, A.M. & Jensen, K.T., 2003. In situ growth of juvenile cockles, *Cerastoderma edule*, experimentally infected with larval trematodes (*Himasthla interrupta*). *Journal of Sea Research*, **50** (1), 37-43.
- Widdows, J. & Navarro, J., 2007. Influence of current speed on clearance rate, algal cell depletion in the water column and resuspension of biodeposits of cockles (*Cerastoderma edule*). *Journal of Experimental Marine Biology and Ecology*, **343** (1), 44-51.
- Wildish, D. & Miyares, M., 1990. Filtration rate of blue mussels as a function of flow velocity: preliminary experiments. *Journal of Experimental Marine Biology and Ecology*, **142** (3), 213-219.
- Wilson, J., 1984. Assessment of the effect of short term salinity changes on the acute oxygen consumption of *Cerastoderma balthica* and *Tellina tenuis* from Dublin Bay. *Journal of Life Sciences Royal Dublin Society*, **5** (1), 57-63.

- Wilson, J.G. & Elkain, B., 1991. Tolerances to high temperature of individual bivalves and the effect of geographic distribution, position on the shore and season. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 169-177.
- Wilson, J.G., 1981. Temperature tolerance of circatidal bivalves in relation to their distribution. *Journal of Thermal Biology*, **6**, 279-286.
- Wilson, J.G., 1993. Climate change and the future for the cockle *Cerastoderma edule* in Dublin Bay - an exercise in prediction modelling. In *Biogeography of Ireland: past, present, and future*, (ed. M.J. Costello & K.S. Kelly), pp. 140-149. Occasional publication of the Irish Biogeographical Society, no. 2. Dublin: Irish Biogeographical Society Ltd.
- Wootton, E., Dyrinda, E., Pipe, R. & Ratcliffe, N., 2003. Comparisons of PAH-induced immunomodulation in three bivalve molluscs. *Aquatic Toxicology*, **65** (1), 13-25.
- Wright, S.L., Rowe, D., Thompson, R.C. & Galloway, T.S., 2013. Microplastic ingestion decreases energy reserves in marine worms. *Current Biology*, **23** (23), R1031-R1033.
- Young, E.F., Bigg, G.R. & Grant, A., 1996. A statistical study of environmental influences on bivalve recruitment in the Wash, England. *Marine Ecology Progress Series*. Oldendorf, **143** (1), 121-129.
- Ysebaert, T., Meire, P., Herman, P.M. & Verbeek, H., 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Marine Ecology Progress Series*, **225**.