



MarLIN

Marine Information Network

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

Common cockle (*Cerastoderma edule*)

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

Dr Harvey Tyler-Walters

2007-06-08

A report from:

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

Please note. This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [<https://www.marlin.ac.uk/species/detail/1384>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

This review can be cited as:

Tyler-Walters, H., 2007. *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.
DOI <https://dx.doi.org/10.17031/marlin.sp.1384.1>



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

(page left blank)



The common cockle *Cerastoderma edule* on mud surface.
 Photographer: Keith Hiscock
 Copyright: Dr Keith Hiscock

See online review for
 distribution map

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

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

Summary

🔍 Description

The familiar edible cockle. The shell is solid, thick, equivalve, globular and broadly oval in outline; up to 5 cm long but usually less. Shell with 22-28 radiating ribs, crossed by conspicuous concentric ridges and may bear short, flat spines. Outer surface off-white, yellowish or brownish. Growth lines are prominent. Inner surface dull white, with a brownish or light purple stain on or about the posterior adductor muscle scar. The pallial line lacks a sinus. Both valves bear two cardinal teeth. In addition the right bear two anterior and two posterior lateral teeth while the left valve bears a single anterior and posterior lateral. Shallow grooves on the inner surface run from the notched margin, fading before reaching the pallial line.

📍 Recorded distribution in Britain and Ireland

Widely distributed in estuaries and sandy bays around the coasts of Britain and Ireland.

📍 Global distribution

Found from the western Barents Sea and northern Norway to the Iberian Peninsula, and south along the coast of west Africa to Senegal.

 **Habitat**

Inhabits the surface of sediments, burrowing to a depth of no more than 5 cm. Found on clean sand, muddy sand, mud or muddy gravel from the middle to lower intertidal, sometimes subtidally. Usually live at salinities between 15 -35 psu but can tolerate salinities as low as 10 psu. Often abundant in estuaries and sheltered bays, and population densities of 10,000 per m² have been recorded.

 **Depth range**

Intertidal

 **Identifying features**

- Shell solid and equivalve; inequilateral with beaks slightly in front of midline (anterior).
- Rounded, strongly convex (globular).
- Shell with 22-28 conspicuous radiating ribs.
- Ligament external.
- Grooves on inner surface of shell running from margin edge to the pallial line; margin crenulate (notched).
- Two adductor muscle scars.
- Pallial line without sinus.
- Right valve with 2 anterior and 2 lateral teeth.
- Left valve with single anterior and posterior laterals.
- Two cardinal teeth present in each valve.

 **Additional information**

Active suspension feeders, living in the top few centimetres of sediment. They are easily dislodged by storms and cockle beds can be washed away during winter gales. Commercially fished in areas such as Morecambe Bay, the Wash, Thames Estuary, Dee Estuary, Outer Hebrides and South Wales.

 **Listed by** **Further information sources**

Search on:

   **NBN WoRMS**

Biology review

☰ Taxonomy

Phylum	Mollusca	Snails, slugs, mussels, cockles, clams & squid
Order	Cardiida	
Family	Cardiidae	
Genus	Cerastoderma	
Authority	(Linnaeus, 1758)	
Recent Synonyms	Cardium edule (Linnaeus, 1758)	

🌿 Biology

Typical abundance	High density
Male size range	ca. 3 -38mm
Male size at maturity	15-20mm
Female size range	15-20mm
Female size at maturity	
Growth form	Bivalved
Growth rate	Variable (see additional text).
Body flexibility	None (less than 10 degrees)
Mobility	
Characteristic feeding method	Active suspension feeder
Diet/food source	
Typically feeds on	Phytoplankton, zooplankton and organic particulate matter.
Sociability	
Environmental position	Infaunal
Dependency	No text entered.
Supports	Host The parasitic copepod <i>Paranthesius rostratus</i> , and the larval stages of various species of digenetic trematode.
Is the species harmful?	No Edible

🏛️ Biology information

Factors affecting growth

Growth rates of *Cerastoderma edule* vary with age, year, season, geographical location, tidal height, temperature regime, food availability, population density and interspecific competition.

- *Cerastoderma edule* grow rapidly in their first 1 -2 years after which growth rate declines with increasing size (Seed & Brown, 1977).
- Growth rates decrease with increasing tidal height, probably due to decreased immersion times and hence reduced food availability at higher shore heights (Richardson *et al.*, 1980; Jensen, 1993; Montaudouin & Bachelet, 1996; Montaudouin, 1996). The highest growth rates in *Cerastoderma edule* were reported in continuously immersed populations

(Guevara & Niell 1989).

- Local variability in growth rate occurs in areas separated by relatively short distances within sites, e.g. Llanrhidian Sands, Wales (Hancock, 1967).
- Growth rates were reported to vary between years and geographical locations (Hancock, 1967; Ducrottoy *et al.*, 1991).
- Growth rates decrease as population density increases probably due to increased competition for food, and direct interference or disturbance due to burrowing and direct contact between individuals (Orton, 1926; Hancock, 1967; Jensen, 1993; Montaudouin & Bachelet, 1996). Montaudouin & Bachelet (1995) reported highest juvenile growth rates at low density (160-200 adults /m²) whereas adult growth rates were only depressed at the highest density examined (2000 adults/m²).
- *Cerastoderma edule* is unable to acclimatise to low temperatures, resulting in reduced metabolic rate and oxygen consumption during winter months. However, reduced food availability in the winter months results in low or negligible growth (Smaal *et al.* 1997).

Seasonal Growth

Growth in *Cerastoderma edule* shows a marked seasonal pattern (Seed & Brown, 1977; Hancock & Franklin, 1972). In the Burry Inlet, Wales, shell growth commenced in May, continued through June until late August after which growth was negligible. Winter growth rates vary, e.g. negligible winter growth occurred for less than a month in the Menai Straits, Wales but for 158 days (between May -October) in Sorbotn, Norway although growth was more vigorous in young (first winter) than older specimens (Richardson *et al.* 1980). Adults may lose weight over winter (Hancock & Franklin, 1972; Newell & Bayne, 1980) probably due to lack of food. Mortality over winter was reported by several authors, e.g. Hancock & Urquhart (1964) report normal winter mortalities of 30 -90% in Burry Inlet, depending on size. After spawning the high food availability and reduced metabolic costs (compared with prior gametogenesis) allows *Cerastoderma edule* to synthesize carbohydrate reserves. The decline in body weight over winter and early spring is associated with the utilisation of lipid, protein and carbohydrate reserves (Newell & Bayne, 1980).

Growth banding

Reduced or negligible winter growth, together with disturbance results in clearly distinguishable external banding. Internal bands are laid down at semi-diurnal intervals related to the tidal cycle. Winter growth and internal bands have been used to age cockles, examine the past history of populations, population dynamics and monitoring (Orton, 1926; Richardson *et al.* 1979; Richardson *et al.*, 1980; Jones & Baxter, 1987a).

Parasitism

Boyden (1972) reported castration of 13% of the population of *Cerastoderma edule* in the River Couch estuary due to infection with larval digenetic trematodes. Jonsson & Andre (1992) suggested that mass mortality of *Cerastoderma edule* occurring on the west coast of Sweden in the summer of 1991 was due to infestation by the larvae of the digenetic trematode *Cercaria cerastodermae* l. *Cercaria cerastodermae* l has been recorded on British shores but was considered rare. The brucephalid cercariae, *Cercaria fulbrighti* primarily occupies digestive gland, foot and gonads. The parasitic copepod *Paranthessius rostratus* was reported in the mantle cavity of cockles around the British Isles (Atkins, 1934) and the Dutch Wadden Sea (sometimes 10s of parasites per individual) (Kristensen, 1958). The rhabdocele *Paravortex cardii* and *Paravortex karlings* have also been reported in *Cerastoderma edule* in the British Isles (Pike & Burt, 1981; Atkins, 1934).



Habitat preferences

Physiographic preferences	Open coast, Strait / sound, Sea loch / Sea lough, Ria / Voe, Estuary, Enclosed coast / Embayment
Biological zone preferences	Lower eulittoral, Mid eulittoral, Sublittoral fringe, Upper eulittoral
Substratum / habitat preferences	Coarse clean sand, Fine clean sand, Muddy gravel, Muddy sand, Sandy mud
Tidal strength preferences	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
Wave exposure preferences	Sheltered
Salinity preferences	Full (30-40 psu), Reduced (18-30 psu), Variable (18-40 psu)
Depth range	Intertidal
Other preferences	No text entered
Migration Pattern	Non-migratory / resident

Habitat Information

Boyden & Russell (1972) compared the habitat preferences of *Cerastoderma edule* and *Cerastoderma glaucum*. They concluded that *Cerastoderma edule* was excluded from hypo- or hyper-saline waters by insufficient tidal flow rather than salinity itself, and that *Cerastoderma edule* was unable to colonize still water conditions. Brock (1979) found *Cerastoderma edule* in Danish fjords with little tidal range and suggested that food availability was more important. However, *Cerastoderma edule* and *Cerastoderma glaucum* may be found together (sympatric), where stable sediments and good food availability occur e.g. *Zostera* sp. covered silt banks (Boyden & Russell, 1972; Brock, 1979).

Predation

Predation has been shown to influence recruitment and population dynamics in *Cerastoderma edule*. (Sanchez-Salazar *et al.*, 1987a; Masski & Guillou, 1999;. Sanchez-Salazar *et al.* (1987a) reported that low shore cockles had high mortalities when small which decreased with size due to predation by shore crab (*Carcinus maenas*) in the summer months that preferred cockles <15 mm in length. Higher on the shore cockle mortality was moderately in the first year (47%) but increased with size, due to predation by oystercatchers (*Haematopus ostralegus*) in the winter months, which prefer cockles of at least 20 mm in length. As a result, the lower shore populations studied were composed of spat and fewer large individuals whereas higher shore populations contained smaller cockles.

Cockles are also preyed on by the shrimp and flatfish, e.g. in Sweden *Crangon crangon* was a dominant predator of cockles <2 mm and cockles were the dominant food for the flounder *Platichthys flesus* (Möller & Rosenberg, 1983). Möller & Rosenberg, (1983) noted that predators removed a significant proportion of bivalve production in years of normal recruitment, less so in years of good recruitment.

Life history

Adult characteristics

Reproductive type	Gonochoristic (dioecious)
Reproductive frequency	Annual protracted

Fecundity (number of eggs)	>1,000,000
Generation time	1-2 years
Age at maturity	18 months
Season	May - June
Life span	5-10 years

Larval characteristics

Larval/propagule type	-
Larval/juvenile development	Planktotrophic
Duration of larval stage	See additional information
Larval dispersal potential	No information
Larval settlement period	May to September but varies (see additional info)

Life history information

Longevity and sexual maturity

Cerastoderma edule may live for up to 9 years or more in some habitats but 2 -4 years is normal. The sex ratio was reported to be 40% males to 60% females (Fretter & Graham, 1964). Adults first mature and spawn in their second summer, at about 18 months old and 15-20 mm in length, however, large cockles (>15 mm) may mature in their first year suggesting that size and maturity are linked (Orton, 1926; Hancock & Franklin, 1972; Seed & Brown, 1977).

Reproductive cycle

Gametogenesis is initiated in winter (October to March) but increases rapidly in spring (February - April) (Newell & Bayne, 1980) and the majority of the population are ripe by mid-summer (Seed & Brown, 1977). Most adults spawn in a short peak period over summer with remaining adults spawning over a protracted period, resulting in a short (ca. 3 month) period of peak settlement followed by generally declining numbers of recruits (Hancock, 1967; Seed & Brown, 1977). Spawning generally occurs between March - August in the UK followed by peak spatfall between May and September, however the exact dates vary between sites in the UK and Europe (Seed & Brown, 1977; Newell & Bayne, 1980). Boyden (1971) suggested that warming of water in spring to 13 °C or above was required to induce spawning, however Ducrottoy *et al.* (1991) suggested that a sudden temperature rise (rather than an absolute level) was probably required to initiate spawning. An occasional late peak in settlement may occur e.g. on the Llanrhidian Sands, Hancock (1967) reported an additional settlement peak in August -September after the main peak in May - July.

Development

Fertilization is external. Males may release about 15 million sperm/sec and females were reported to release about 1900 eggs/sec. Gamete viability is short and André & Lindegarth (1995) found that fertilization was reduced to 50% in 2 hours and that no fertilization was observed after 4 -8 hrs. André & Lindegarth (1995) noted that fertilization efficiency was dependant 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. Eggs (50-60 µm) develop into a trochophore stage within the egg membrane and then into a typical bivalve veliger at ca. 80 µm, the D-larvae (so called due to the D-shaped shell) after about 3 -4 days the foot develops and the veliger metamorphoses into a juvenile cockle (pediveliger) at ca. 270 µm after about 3 -5 weeks (Lebour, 1938; Creek, 1960). The juveniles reach ca. 600-700 µm after about 3 weeks, and by 3 months are

ca. 0.75-1.5 mm long (Creek, 1960).

Recruitment

Settlement and subsequent recruitment has a significant impact on the dynamics of *Cerastoderma edule* populations, in many but not all circumstances (Olafsson *et al.*, 1994). Settlement and recruitment is sporadic and varies with geographic location, year, season, reproductive condition of the adults and climatic variation. Factors reported to affect recruitment follow.

- Geographical location (Ducrotoy *et al.* 1991; Olafsson *et al.*, 1994).
- Annual variation in climate. Ducrotoy *et al.* (1991) reported the variation in annual recruitment between years for several sites in Europe, and noted a correlation between good recruitment and a previous severe winter (presumably due to high adult mortality, reduced population density of adults and reduced numbers of infaunal predators), in many but not all cases.
- Good recruitment was also observed after heavy storm surges reduced the adult population (Ducrotoy *et al.* 1991).
- Post-settlement erosion and surface sediment erosion by currents and storms. Juveniles may be transported by currents until 2mm in size and high densities of juveniles may be swept away by winter storms resulting in subsequent patterns of adult distribution (Olafsson *et al.*, 1994).
- Post-settlement mortalities of 60-96% have been reported, resulting from intra and interspecific mortality and predation (Sanchez-Salazar *et al.*, 1987a; Montaudouin & Bachelet, 1996; André *et al.*, 1993; Guillou & Tartu, 1994).
- Adult suspension feeders, including adult cockles, may reduce settlement by ingestion of settling larvae and juveniles or smothering by sediment displaced in burrowing and feeding (Montaudouin & Bachelet, 1996). Therefore, recruitment may be dependant on adult population density (André *et al.*, 1993). André *et al.* (1993) observed that adults inhaled 75% of larvae at 380 adults/m², which were also ingested. However, Montaudouin & Bachelet, (1996) noted that adults that inhaled juveniles, rejected them and closed their siphons but that rejected juveniles usually died.
- Predation (see distribution) (Dame, 1996; Sanchez-Salazar *et al.* 1987a).
- Guillou & Tartu (1994) noted that spat also suffered from mortality in their first year in the spring following their settlement, even through food was available, probably due to exhausted energy reserves (after winter) and spring predation from shore crabs.

Ducrotoy *et al.* (1991; Figure 14) identified, 'crisis', 'recovery', 'upholding', and 'decline' phases in dynamics of *Cerastoderma edule* populations. Each phase is characterised by:

- 'Crisis': a few age classes and successive spawnings and maximal growth due to low density;
- 'Recovery': single high density recruitment to first year class (breeding stocks may be synchronised by severe temperatures);
- 'Upholding': several age classes, higher densities of older age classes, seasonal recruitment, and low growth rate;
- 'Decline': reducing abundance, adult mortality or unsuccessful recruitment due to climatic factors, lower food levels, competition or parasitic infection.

Ducrotoy *et al.* (1991) suggested that increased growth rate indicated instability. Any population may exhibit these characteristics at different times or location.

Sensitivity review

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

A Physical Pressures

	Intolerance	Recoverability	Sensitivity	Confidence
Substratum Loss	High	High	Moderate	Moderate

Loss of the substratum will also remove the resident population of *Cerastoderma edule*. Hall & Harding (1997) found that *Cerastoderma edule* abundance had returned to control levels within about 56 days after significant mortality due to suction dredging, and Moore (1991) also suggested that recovery was rapid. Recovery is dependant on recruitment of spat or migration (active or passive) from the surrounding substratum. For example, Coffen-Smout & Rees (1999) reported that cockles could be distributed by flood and ebb tides, but especially flood tides (by rolling around the surface) up to 0.45 m on neap tides or between 94 m and 164 m on spring tides and could colonize cleared areas at a rate of 2.2 -12 individuals/m²/14 days. It seems likely therefore that the population could recover within a year, however, given the sporadic nature of recruitment in *Cerastoderma edule*, recovery may be more protracted.

Smothering	Intermediate	High	Low	Moderate
-------------------	--------------	------	-----	----------

Cerastoderma edule has short siphons and needs to keep in contact with the surface of the sediment. Richardson *et al.* (1993(b)) reported that they burrow quickly to the surface if covered by 2 cm of sediment (under laboratory or field conditions) when emmersed (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(b)) suggested that surface movement in darkness, perhaps accompanied by passive movement if rolled by flood and ebb tides might be a response to avoiding areas of disturbed sediment. Jackson & James reported that few *Cerastoderma edule* buried to 10 cm in sediment were able to burrow to the surface whereas most buried to a depth of 5 cm could reach the surface. In another experiment *Cerastoderma edule* buried 10 cm in sandy substrate was able to burrow near to the surface, but still suffered 83% mortality in 6 days, whereas in muddy substrates all cockles died between 3 and 6 days. Experimental baiting digging resulted in significant mortality 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). Smaller individuals were more likely to die than larger ones. Fowler (1999) cites reports of 90% mortality of cockles in areas affected by bait digging, recolonization occurring three months after bait digging, although the cockle population structure was still different from undisturbed areas. Therefore, cockles are probably of intermediate intolerance to smothering by 5 cm of sediment although smaller individuals may be more intolerant. No information on smothering and spat was found. In years of good recruitment recovery may occur within a year, however, recruitment is sporadic (see reproduction) and may take longer in 'bad' years.

Increase in suspended sediment	Low	Immediate	Not sensitive	Moderate
---------------------------------------	-----	-----------	---------------	----------

Cerastoderma edule is adapted to life in a sedimentary environment and quite capable of burrowing. Increasing total particulate concentrations have been shown to decrease

clearance rates and increase pseudofaeces production (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 & Widdows (1997) suggested that *Cerastoderma edule* was able to compensate for decrease in particulate quality (i.e. proportion of organic to inorganic seston) between 1.6 to 300 mg/l. This was accomplished by an effective preingestive selection of organic particulates, together with increasing filtration and rejection rates. Navarro & Widdows (1997) concluded that *Cerastoderma edule* was well adapted to living in turbid environments such as intertidal mudflats. Increased siltation and suspended sediment concentration results 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.

Decrease in suspended sediment

Desiccation

Intermediate

High

Low

Moderate

When emersed *Cerastoderma edule* gapes, actively expels water from the mantle cavity, and takes in a bubble of air. In the laboratory, emersed *Cerastoderma edule* absorbed oxygen from the enclosed air bubble, probably through the mantle and mantle edges, and took in another bubble within 2 hrs (Boyden, 1971). However, when immersed *Cerastoderma edule* exhibited an oxygen debt, suggesting that some anaerobic respiration had occurred (Boyden, 1971; Widdows & Shick, 1985). Boyden (1971) reported that *Cerastoderma edule* survived 42.9% water loss. *Cerastoderma edule* is likely to be protected from significant desiccation due to its infaunal habit and the humidity of the surrounding sediment (Boyden, 1971; Widdows & Shick, 1985). However, increased desiccation, equivalent to raising the population from mid to high water is likely to reduce the species abundance and the extent of the population. The population could probably recover within a year, however, given the sporadic nature of recruitment in *Cerastoderma edule*, recovery may be more protracted.

Increase in emergence regime

Intermediate

High

Low

Low

Cerastoderma edule is found from high water to the sublittoral fringe although its highest abundance occurs at mid tidal level. *Cerastoderma edule* is capable of aerial respiration when emersed at low tide, by gaping, and like most bivalve molluscs is capable of anaerobic respiration (Boyden, 1972; Widdows & Shick, 1985). Boyden (1972) noted that on emersion the cockle actively takes air into the mantle cavity, which may be replaced within 2hrs if still emersed. The bubble is ejected upon immersion. Increased emergence is likely to depress this species height on the shore due to increased exposure to temperature extremes (see temperature) and desiccation (see above), however this may be countered by its extent at the bottom of the shore. Decreased emergence, perhaps as a result of sea level rise may result in a reduction in intertidal area and, therefore, a decrease in available habitat (Wilson, 1993).

Decrease in emergence regime

Increase in water flow rate

Intermediate

High

Low

Low

The hydrodynamic regime strongly influences the sediment structure, oxygenation, food supply and recruitment. 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 & Rees (1999) reported that cockles could be distributed

by flood and ebb tides, but especially flood tides (by rolling around the surface) up to 0.45 m on neap tides or between 94 m and 164 m on spring tides. Newly settled spat and juveniles (<4.8 mm) are capable of bysso-pelagic dispersal. Therefore, water flow rates probably affect the distribution and dispersal of juveniles and adults. More importantly increased water flow rate is likely to increase the grain size of the sediment. *Cerastoderma edule* prefers muddy-sand to sandy-mud substrates. Decreasing water flow rate may increase siltation and favour muddy substrates that are unsuitable for *Cerastoderma edule*. Boyden & Russell (1972) suggested that lack of tidal flow may exclude *Cerastoderma edule* possibly due to reduced food availability as suggested by Brock, (1979). Therefore, decreased water flow rates may exclude *Cerastoderma edule* from the affected area.

Decrease in water flow rate

Increase in temperature

Intermediate

High

Low

Moderate

High mortalities of cockle populations due to severe winters have been reported by many authors (Kristensen, 1958; Hancock & Urquhart, 1964; Beukema, 1990; Ducrotoy *et al.*, 1991). 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. Beukema (1990) considered *Cerastoderma edule* to be intolerant of cold winters. Kristensen (1958) reported that *Cerastoderma edule* from the Dutch Wadden Sea died within 24 hrs at -1.9°C with 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 a upper lethal temperature of 42.5°C. Wilson (1981) noted that *Cerastoderma edule* had limited ability to acclimate. 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. *Cerastoderma edule* larvae showed optimal growth between 15 and 20°C, but poor or erratic growth at 10°C or 30°C (Kingston, 1974). 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 intolerance of *Cerastoderma edule* to temperature change will be dependant on season, an acute short term temperature rise in summer or decrease in winter may be detrimental. However, *Cerastoderma edule* may be tolerant to long-term temperature increases although decreasing temperatures are likely to result in more frequent freezing events in winter. Therefore, *Cerastoderma edule* is probably highly intolerant of acute decreases in temperature in winter or summer months. Rapid increases in temperature during the spawning season may initiate spawning (Ducrotoy *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 its close contact with the sediment surface. The observed high mortalities in winter months may be due to low food availability and predation rather than temperature alone, except in severe winters. The upper

lethal temperature of 42.8°C is unlikely to occur on mudflats except in extremely hot summers. Therefore, an intolerance of intermediate rather than high has been reported. Beukema (1990) reported that the biomass and species richness of winter tidal-flat zoobenthos was restored within 1-2 years after severe winters in the Dutch Wadden Sea. The population could probably recover within a year, however, given the sporadic nature of recruitment in *Cerastoderma edule*, recovery may be more protracted and, therefore, recovery has been assessed as 'high'.

Decrease in temperature

Increase in turbidity Tolerant Not relevant Not sensitive Not relevant

Increasing turbidity may reduce phytoplankton productivity and hence decrease food availability, however *Cerastoderma edule* is capable of ingesting organic seston (see siltation) 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.

Decrease in turbidity

Increase in wave exposure Intermediate High Low Low

Changes in wave exposure are likely to have marked effects on the sediment dynamics of the shore. Increased exposure will 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. Increased wave exposure is also likely to remove adult cockles from the sediment surface which may be subsequently lost from the population (see water flow rate).

Decrease in wave exposure

Noise Tolerant Not relevant Not sensitive High

Cerastoderma edule can probably detect the vibration caused by predators and will withdraw its siphons. However, little information was found concerning the effect of noise or vibration on cockle populations and it is unlikely to be sensitive to noise or vibration.

Visual Presence Tolerant Not relevant Not sensitive High

Cerastoderma edule has well developed eyes on the sensory tentacles of the inhalant and exhalant tentacles (Charles, 1966). These probably enable the cockle to respond to shadowing by predators and withdraw the siphons. However its visual acuity is probably limited and it is unlikely to be sensitive to visual presence.

Abrasion & physical disturbance Intermediate High Low Moderate

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). Physical disturbance equivalent to a passing scallop dredge is likely to cause a similar degree of damage. Therefore an intolerance of intermediate has been recorded. Recoverability is likely to be high (see additional information below).

Displacement Low High Low Moderate

Coffen-Smout & Rees (1999) noted that cleared areas of sediment could be recolonized by 2.2

-12 cockles /m² / 14 days. They also reported that cockles could be distributed by flood and ebb tides, but especially flood tides (by rolling around the surface) up to 0.45 m on neap tides or between 94 m and 164 m on spring tides. Similarly, 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. Disturbance and displacement may also reduce the growth rates (Orton, 1926) or interfere with the reproductive cycle (Hummel & Bogaards, 1989). Cockles on the surface of the sediment, are at an increased risk of predation, depending on the time of day, light, and tide. However, populations of cockles are probably moved, buried or displaced naturally by storms and once exposed can burrow relatively quickly into suitable sediment, and therefore are probably adapted to being displaced. Reduction in the local population density may enable good recruitment in following years, dependent on larval supply.

Chemical Pressures

	Intolerance	Recoverability	Sensitivity	Confidence
Synthetic compound contamination	Intermediate	High	Low	Very low

Bryan & Gibbs (1991) reported evidence suggesting that TBT may be responsible for recruitment failure, due to either reproductive failure or larval mortality in bivalve molluscs, e.g. *Pecten maximus* at ca. 50 ng/l TBT. *Cerastoderma edule* was reported to accumulate PCBs from ingestion of contaminated particulates but no biological effects were described (Langston, 1978). However, little other information concerning the effects of synthetic chemicals was found. Recruitment failure in *Cerastoderma edule* may be significant due to the natural high levels of winter mortality and could result in decline of the local population, therefore an intolerance of intermediate is reported, albeit at very low confidence.

Heavy metal contamination	Intermediate	High	Low	Moderate
----------------------------------	--------------	------	-----	----------

Bryan (1984) states that Hg is the most toxic metal to bivalve molluscs while Cu, Cd and Zn seem to be most problematic in the field. In bivalve molluscs Hg was reported to have the highest toxicity, mortalities occurring above 0.1-1 µg/l after 4-14 days exposure (Crompton, 1997), toxicity decreasing from Hg > Cu and Cd > Zn > Pb and As > Cr (in bivalve larvae, Hg and Cu > Zn > Cd, Pb, As, and Ni > to Cr). Although Hg concentrations in *Cerastoderma edule* were found to increase with proximity to industrial discharges in Limfjord, Denmark, Cd and Pb showed no such relationship (Brock, 1992), however, laboratory exposure to 100 ppb Hg (as HgCl₂) for 32 days did not affect growth. Brock (1992) isolated a metallothionein-like protein that may be involved in detoxification. Jenner & Bowmer (1990) exposed cockles to different proportions of pulverised fuel ash (PFA) from a coal powered power station, which contained a variety of heavy metals. Exposure to 100% PFA resulted in 43.3% mortality after 90 days, whereas regular addition of PFA to the surface of uncontaminated sediment resulted in 71% mortality in 90 days. *Cerastoderma edule* accumulated Zn and Ni but not As, Cu, Cr or Sb in their experiments. However, the observed mortality could be due to PFA being an unsuitable sediment. Wilson (1983) demonstrated that *Cerastoderma edule* accumulated Ni, but suffered no mortality at 100 µg/l or associated change in body condition or respiration. Wilson (1983) suggested that *Cerastoderma edule* may be a suitable indicator species for Ni. 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.*, 1991(a), (b)).

Transplantation of *Cerastoderma edule* into Restronguet Creek (highly polluted by heavy metals) resulted in 10-15% mortality within 63 days but 100% within ca. 4 months (Bryan & Gibbs, 1983). Bryan & Gibbs (1983) report that *Cerastoderma edule* takes up heavy metals mainly from solution rather than from sediment. They concluded that the toxic body load for Cu in *Cerastoderma edule* was ca. 250 µg/g tissue and that it was excluded from Restronguet Creek by the high levels of Cu and Zn.

Hydrocarbon contamination

Intermediate

High

Low

Low

Savari *et al.* (1991(a)) stated there was a concentration related reduction in scope for growth of *Cerastoderma edule* with increasing concentration of hydrocarbons in the water column. Timmermans *et al.* (1996) noted a reduction in gonad development and percentage fertilization exposed for 9 months to Rotterdam harbour sediment contaminated with PCBs, PAHs, Cd, Hg, Pb and Zn, probably due to an increased level of parasitism (and presumably susceptibility to parasites) in the polluted specimens with respect to the control. However, no significant difference in larval development was found. 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). 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 (SEEEC, 1998). Therefore, an intermediate intolerance has been reported.

Radionuclide contamination

Not relevant

Miramand & Germain (1985) examined the uptake of plutonium 239 and americium 241 in *Cerastoderma edule*. They showed that americium 241 was taken up preferentially to plutonium 239, from water (and interstitial water), rather than from sediment. Americium 241 accumulated mainly in the tissues of the digestive tract while plutonium 239 accumulated mainly in the shell. Chassaud-Bouchard (1992) demonstrated similar accumulation of americium 241, plutonium 239 and uranium 238. Chassaud-Bouchard (1992) also reported that uptake of these nuclides resulted in damage to the nucleus, increased activity of the golgi apparatus and decreased numbers of mitochondria in the cells of the bivalves studied. However, the evidence was not clearly presented and its ecological significance was not addressed.

Changes in nutrient levels

Intermediate

High

Low

Moderate

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 & 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. It is likely that increased nutrient levels leading to eutrophication may contribute indirectly to mass mortalities in *Cerastoderma edule* populations.

Increase in salinity

Low

Very high

Very Low

Moderate

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 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. Field observations by Russell & Petersen (1973) demonstrated that *Cerastoderma edule* died when transplanted to Widewater lagoon. Kristensen (1958) reported 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. Kingston (1974) found that *Cerastoderma edule* larvae grew optimally at 30 and 35 psu, but were frequently deformed at 20 psu. and did not metamorphose at 45 psu. 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. *Cerastoderma edule* are primarily intertidal and exposed to heavy rainfall, freshwater runoff, evaporation and potential hypo-saline conditions. The studies reported above show a wide tolerance range of salinity for both adults and larvae.

Decrease in salinity

Changes in oxygenation

High

High

Moderate

Moderate

McMahon & Wilson (1981) pointed out that the surface water film on sand flats have oxygen concentration at or above atmospheric saturation, which was reduced to 9.7 -25.2% saturation at 2 cm depth and 4.6-7.2% saturation at 5cm. Therefore, *Cerastoderma edule* rarely encounters hypoxic or anoxic conditions, although Rosenberg & Loo (1988) document decreased oxygen levels of surface waters in the Kattegat. Boyden (1972) reported that emersed, air breathing *Cerastoderma edule* had a median lethal survival time of 129 hrs, whereas specimens unable to 'breathe' air (clamped) or in an oxygen free environment had median lethal times of 69 and 75 hrs respectively, indicating that *Cerastoderma edule* was capable of anaerobic respiration. Rosenberg *et al.* (1991) reported 100% mortality of *Cerastoderma edule* exposed to 0.5 - 1.0 ml/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 ml/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 several days anoxia but it is likely that continued exposure to 2 mg/l oxygen for a week would be lethal.

Biological Pressures

Intolerance

Recoverability

Sensitivity

Confidence

Introduction of microbial pathogens/parasites

Intermediate

High

Low

Moderate

Jonsson & Andre (1992) suggested that mass mortality of *Cerastoderma edule* occurring on the west coast of Sweden in the summer of 1991 was due to infestation by the larvae of the digenean trematode *Cercaria cerastodermae* I. However, *Cercaria cerastodermae* I was considered rare in the British Isles. *Cerastoderma edule* may be infected by numerous larval digenean trematodes, and the parasitic copepod *Paranthessius rostratus* (see General Biology). No evidence of mass mortality of cockles in the British Isles due to parasites was found but

Boyden (1972) reported castration of a population of cockles in the river Couch. Parasites undoubtedly reduce the condition and reproductive potential of infected *Cerastoderma edule*. Therefore, parasites are likely to directly or indirectly result in a reduction in the abundance and extent of a population of *Cerastoderma edule*.

Introduction of non-native species

Not relevant

No information regarding alien or non-native species likely to compete with or exclude *Cerastoderma edule* was found.

Extraction of this species

Intermediate

High

Low

Moderate

Hall & Harding (1997) examined the effects of hydraulic and tractor dredging of *Cerastoderma edule* on macrobenthic communities. They concluded that although significant mortality of *Cerastoderma edule* and other infauna occurred, recovery was rapid and the overall effects on populations was low. Hall & Harding (1997) found that *Cerastoderma edule* abundance had returned to control levels within about 56 days and Moore (1991) also suggested that recovery was rapid. Cotter *et al.* (1997) noted that tractor dredging reduced the *Cerastoderma edule* stock by 31-49% depending on initial density, while Pickett (1973) reported that hydraulic dredging removed about one third of the cockle fishery. 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 subsequent settlement was good especially in areas of previously high population density, however, Franklin & Pickett (1978) noted that subsequent spat survival was markedly reduced. Cotter *et al.* (1997) reported appreciable loss of spat and juveniles, partly due increased predation of exposed juveniles. Pickett (1973) also noted reduced survivability of 1-2 year old cockles after hydraulic dredging. However, most studies concluded that the impact of mechanised dredging on cockle populations and macrofauna in the long term was low (Pickett, 1973; Franklin & Pickett, 1978; Cook, 1990; Moore, 1991; Cotter *et al.*, 1997; Hall & Harding, 1997; Ferns *et al.*, 2000). Time of year of exploitation will influence recovery and avoiding seasonal spawning or larval settlement periods is likely to reduce the time taken for recovery (Gubbay & Knapman, 1999). Cockle beds have been mechanically fished for decades but several beds are closed from time to time depending on settlement and recruitment to the population, which is sporadic (see importance). Recovery may take less than a year in years of good recruitment but longer in bad years, therefore a recoverability of high has been used.

Extraction of other species

High

High

Moderate

High

Experimental baiting digging resulted in significant mortality in areas 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). Smaller individuals were more likely to die than larger ones. Fowler (1999) cites reported 90% mortality of cockles in areas affected by bait digging, recolonization occurring three months after bait digging, although the cockle population was still different from undisturbed areas. Jackson & James (1979) pointed out that bait digging disturbs sediment to a depth of 30-40 cm and probably buries many cockles below 10 cm and surface exposure of others that are then taken by predators. They suggested that bait digging was involved in the decline in the cockle fishery on the north Norfolk Coast in the 1950s and 60s. Therefore, cockles are probably of high intolerance to bait digging although smaller individuals may be more intolerant. In years of good recruitment recovery may occur within a year, however, recruitment is sporadic (see reproduction) and may take longer in 'bad' years.

Additional information

None

Importance review

Policy/legislation

- no data -

Status

National (GB)
importance

-

Global red list
(IUCN) category

-

Non-native

Native

-

Origin

-

Date Arrived

-

Importance information

Commercial beds of the edible cockle *Cerastoderma edule* are fished in the Wash, Thames estuary, Morecambe Bay, Dee estuary, and Ribble estuary in England, the Burry Inlet, South Wales, and Solway Firth, Scotland. Cockles of 20-25 mm are taken commercially. More cockles are landed in Britain than any other mollusc, e.g. 22,329 tonnes of cockles in were landed 1994 (Edwards, 1997). Traditional hand raking collection methods have been superseded by mechanised methods such as tractor dredging or hydraulic dredging techniques, except in the Burry Inlet, South Wales. Demand for cockle meat in Holland and Spain, have increased, especially since the collapse of stocks in Wadden Sea in the late 1980s. Hence landings have increased since the 1960s to about 30 -40,000 tonnes per annum in late 1990s (Edwards, 1997; Hall & Harding, 1997). Mechanised methods are more efficient than hand raking and capable of exploiting lower density beds but have the potential to over-fish the cockle stocks without adequate management (Pickett, 1973; Franklin & Pickett, 1978).

Concerns about possible over-exploitation and large scale dredging operations on cockle stocks and other infauna has led to restriction of numbers collected and/or the method used. For example, dredging by any vehicle is prohibited in Scotland, some Sea Fisheries Committees in England and Wales specify the type or design of equipment used and hand gathering is the only permitted method in some areas (Gubbay & Knapman, 1999).

Bibliography

- 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., Boday, A. & Masse, H., 1981. Upper temperature tolerances of some European Mollusca III. *Cardium glaucum*, *C. tuberculata* and *C. edule*. *Marine Biology*, **65**, 177-183.
- Atkins, D., 1934. Two parasites of the common cockle, *Cardium edule*; a rhabdocoel *Paravortex cardii* Halley and a copepod *Paranthassius rstatus* (Cann.). *Journal of the Marine Biological Association of the United Kingdom*, **19**, 669-676.
- 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.
- 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.
- Boyden, C.R., 1972. Behaviour, survival and respiration of the cockles *Cerastoderma edule* and *C. glaucum* in air. *Journal of the Marine Biological Association of the United Kingdom*, **52**, 661-680.
- Brock, V., 1979. Habitat selection of two congeneric bivalves, *Cardium edule* and *C. glaucum* in sympatric and allopatric populations. *Marine Biology*, **54**, 149-156.
- Brock, V., 1992. Effects of mercury on the biosynthesis of porphyrins in bivalve molluscs (*Cerastoderma edule* (L.) and *Cerastoderma lamarcki* (Reeve)). *Journal of Experimental Marine Biology and Ecology*, **164**, 17-29.
- Bryan, G.W. & Gibbs, P.E., 1983. *Heavy metals from the Fal estuary, Cornwall: a study of long-term contamination by mining waste and its effects on estuarine organisms*. Plymouth: Marine Biological Association of the United Kingdom. [Occasional Publication, no. 2.]
- Bryan, G.W. & Gibbs, P.E., 1991. Impact of low concentrations of tributyltin (TBT) on marine organisms: a review. In: *Metal ecotoxicology: concepts and applications* (ed. M.C. Newman & A.W. McIntosh), pp. 323-361. Boston: Lewis Publishers Inc.
- Charles, G.H., 1966. Sense organs (less Cephalopods). In *Physiology of Mollusca*, vol. 2 (ed. K.M. Wilbur & C.M. Yonge), pp. 455-521. New York: Academic Press.
- Chassaud-Bouchard, C., 1992. Biological effects of uranium and transuranium nuclides on marine bivalves *Mytilus edulis*, *Crassostrea gigas* and *Cerastoderma edule*: microanalysis at the cellular and subcellular levels. In *Proceedings of the FAO/UNEP/IOC Workshop on the biological effects of pollutants on marine organisms, 10-14 September 1991, Malta*. (ed. G.D. Gabrielides). (MAP Technical Report Series, no. 69.), Athens: UNEP.
- Cook, W., 1990. Studies on the effects of hydraulic dredging on cockle and other macroinvertebrate populations 1989-1990. *North Western and North Wales Sea Fisheries Committee*.
- 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.
- Creek, G.A., 1960. The development of the lamellibranch *Cardium edule* L. *Proceedings of the Zoological Society of London*, **135**, 243-260.
- Dame, R.F.D., 1996. *Ecology of Marine Bivalves: an Ecosystem Approach*. New York: CRC Press Inc. [Marine Science Series.]
- Diaz, R.J. & Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review*, **33**, 245-303.
- Ducrottoy, C.R., Rybarczyk, H., Souprayen, 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.
- Edwards, E., 1997. Molluscan fisheries in Britain. In *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central American and Europe*, vol. 3, *Europe*, (ed. C.L. MacKenzie, Jr., V.G. Burrell, Jr., Rosenfield, A. & W.L. Hobart). *National Oceanic and Atmospheric Administration*, NOAA Technical Report NMFS 129.
- 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.
- Fowler, S.L., 1999. Guidelines for managing the collection of bait and other shoreline animals within UK European marine sites. *Natura 2000 report prepared by the Nature Conservation Bureau Ltd. for the UK Marine SACs Project*, 132 pp., Peterborough: English Nature (UK Marine SACs Project), <http://www.english-nature.org.uk/uk-marine/reports/reports.htm>
- 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.
- Fretter, V. & Graham, A., 1964. Reproduction. In *Physiology of Mollusca*, vol. 1, (ed. K.M. Wilbur & C.M. Yonge). New York: Academic Press.
- Gubbay, S., & Knapman, P.A., 1999. *A review of the effects of fishing within UK European marine sites*. Peterborough, English Nature.
- Guevara, F.M. & Niell, F.X., 1989. Growth rates in a continuously immersed population of *Cerastoderma edule* (L.). *Scientia Marina*,

53, 483-489.

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, 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. & Franklin, A., 1972. Seasonal changes in the condition of the edible cockle *Cardium edule* (L.). *Journal of Applied Ecology*, **9**, 567-579.

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.

Hancock, D.A., 1967. Growth and mesh selection in the edible cockle (*Cardium edule* L.). *Journal of Applied Ecology*, **4**, 137-157.

Hayward, P., Nelson-Smith, T. & Shields, C. 1996. *Collins pocket guide. Sea shore of Britain and northern Europe*. London: HarperCollins.

Hayward, P.J. & Ryland, J.S. (ed.) 1995b. *Handbook of the marine fauna of North-West Europe*. Oxford: Oxford University Press.

Hummel, H. & Bogaards, R.H., 1989. Changes in the reproductive cycle of the cockle *Cerastoderma edule* after disturbance by means of tidal manipulation. In *Proceedings of the 23rd European Marine Biology Symposium, School of Biological Sciences, University of Wales Swansea, 5-9 September 1988. Reproduction, Genetics and Distribution of Marine Organisms*, (ed. J.S. Ryland & P.A. Tyler), p.133-136. Denmark: Olsen & Olsen.

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.

Jenner, H.A. & Bowmer, T., 1990. The accumulation of metals and their toxicity in the marine intertidal invertebrates *Cerastoderma edule*, *Macoma balthica*, *Arenicola marina* exposed to pulverised fuel ash in mesocosms. *Environmental Pollution*, **66**, 139-156.

Jensen, K.T., 1993. Density dependant growth in cockles (*Cerastoderma edule*): evidence from interannual comparisons. *Journal of the Marine Biological Association of the United Kingdom*, **73**, 333-342.

Johnstone, J., 1899. *Cardium*. Liverpool: Liverpool Marine Biology Committee. [L.M.B.C. Memoirs II].

Jones, A.M. & Baxter, J.M., 1987a. Monitoring and surveillance of sandy shores using the bivalve *Cerastoderma edule* (L.). In *Proceedings of the Estuarine and Brackish Water Association, ESBA 17 Symposium, 14-18 September 1987, University of Dundee, Dundee. Developments in estuarine and coastal techniques*, (ed. J. McManus & M. Elliot), pp. 63-68. Denmark: Olsen & Olsen.

Jonsen, 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.

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.

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

Langston, W.J., 1978. Accumulation of polychlorinated biphenyls in the cockle *Cerastoderma edule* and the tellin *Macoma balthica*. *Marine Biology*, **45**, 265-272.

Lebour, M.V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. *Journal of the Marine Biological Association of the United Kingdom*, **23**, 119-144.

Masski, H. & Guillou, J., 1999. The role of biotic interactions in juvenile mortality of the cockle (*Cerastoderma edule* L.): Field observations and experiment. *Journal of Shellfish Research*, **18**, 575-578.

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.

McMahon, R.F. & Wilson, J.G., 1981. Seasonal respiratory responses to temperature and hypoxia in relation to burrowing depth in three intertidal bivalves. *Journal of Thermal Biology*, **6**, 267-277.

Miramand, P. & Germain, P., 1985. Sea water uptake, sediment transfer and histo-autoradiographic study of plutonium (²³⁹Pu) and americium (²⁴¹Am) in the edible cockle *Cerastoderma edule*. *Marine Ecology Progress Series*, **22**, 59-68.

Möller, P. & Rosenberg, R., 1983. Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow waters, western Sweden. *Ophelia*, **22**, 33-35.

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.

Montaudouin de X., 1996. Factors involved in growth plasticity of cockles *Cerastoderma edule* (L.), identified by field survey and transplant experiments. *Journal of Sea Research*, **36**, 251-265.

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.

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.
- Olafsson, E.B., Peterson, C.H. & Ambrose, W.G. Jr., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology: an Annual Review*, **32**, 65-109
- Orton, J.H., 1926. On the growth rate of *Cardium edule*, part 1. Experimental observations. *Journal of the Marine Biological Association of the United Kingdom*, **14**, 239-280.
- 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.
- Pike, A.W. & Burt, M.D.B., 1981. *Paravortex karlingi* sp. nov. from *Cerastoderma edule*. *Hydrobiologia*, **84**, 23-30.
- Richardson, C.A., Crisp, D.J. & Runham, N.W., 1979. Tidally deposited growth bands in the shell of the common cockle *Cerastoderma edule* (L.). *Malacologia*, **18**, 277-290.
- Richardson, C.A., Crisp, D.J., Runham, N.W. & Gruffydd, Ll. D., 1980. The use of tidal growth bands in the shell of *Cerastoderma edule* to measure seasonal growth rates under cool temperate and sub-arctic conditions. *Journal of the Marine Biological Association of the United Kingdom*, **60**, 977-989.
- 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.
- 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.
- 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.
- 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.
- Seaward, D.R., 1982. *Sea area atlas of the marine molluscs of Britain and Ireland*. Peterborough: Nature Conservancy Council.
- Seaward, D.R., 1990. *Distribution of marine molluscs of north west Europe*. Peterborough: Nature Conservancy Council.
- Seed, R. & Brown, R.A., 1977. A comparison of the reproductive cycles of *Modiolus modiolus* (L.), *Cerastoderma* (= *Cardium*) *edule* (L.), and *Mytilus edulis* L. in Strangford Lough, Northern Ireland. *Oecologia*, **30**, 173-188.
- SEEEC (Sea Empress Environmental Evaluation Committee), 1998. The environmental impact of the Sea Empress oil spill. *Final Report of the Sea Empress Environmental Evaluation Committee*, 135 pp., London: HMSO.
- 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.
- Tebble, N., 1976. *British Bivalve Seashells. A Handbook for Identification*, 2nd ed. Edinburgh: British Museum (Natural History), Her Majesty's Stationary Office.
- 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.
- Timmermans, B.M.H., Hummel, H. & Bogaards, R.H., 1996. The effect of polluted sediment on the gonadal development and embryogenesis of bivalves. *Science of the Total Environment*, **187**, 231-236.
- Widdows, J & Shick, J.M., 1985. Physiological responses of *Mytilus edulis* and *Cardium edule* to aerial exposure. *Marine Biology*, **85**, 217-232.
- 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., 1983. The uptake and accumulation of Ni by *Cerastoderma edule* and its effect on mortality, body condition and respiration rate. *Marine Environmental Research*, **8**, 129-148.
- 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.

Young, C.M., 1995. Behaviour and locomotion during the dispersal phase of larval life. In *Ecology of Marine Invertebrate Larvae*, (ed. L. McEdward), Chapter 8, pp. 249-277. New York: CRC Press Inc. [Marine Science Series].

Datasets

Bristol Regional Environmental Records Centre, 2017. BRERC species records recorded over 15 years ago. Occurrence dataset: <https://doi.org/10.15468/h1n5p> accessed via GBIF.org on 2018-09-25.

Centre for Environmental Data and Recording, 2018. IBIS Project Data. Occurrence dataset: <https://www.nmni.com/CEDaR/CEDaR-Centre-for-Environmental-Data-and-Recording.aspx> accessed via NBNAtlas.org on 2018-09-25.

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

Cofnod – North Wales Environmental Information Service, 2018. Miscellaneous records held on the Cofnod database. Occurrence dataset: <https://doi.org/10.15468/hcgqsi> accessed via GBIF.org on 2018-09-25.

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

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

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

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

Fife Nature Records Centre, 2018. St Andrews BioBlitz 2014. Occurrence dataset: <https://doi.org/10.15468/erweal> accessed via GBIF.org on 2018-09-27.

Fife Nature Records Centre, 2018. St Andrews BioBlitz 2015. Occurrence dataset: <https://doi.org/10.15468/xtrbvy> accessed via GBIF.org on 2018-09-27.

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

Lancashire Environment Record Network, 2018. LERN Records. Occurrence dataset: <https://doi.org/10.15468/esxc9a> accessed via GBIF.org on 2018-10-01.

Manx Biological Recording Partnership, 2017. Isle of Man wildlife records from 01/01/2000 to 13/02/2017. Occurrence dataset: <https://doi.org/10.15468/mopwow> accessed via GBIF.org on 2018-10-01.

Manx Biological Recording Partnership, 2018. Isle of Man historical wildlife records 1995 to 1999. Occurrence dataset: <https://doi.org/10.15468/lo2tge> accessed via GBIF.org on 2018-10-01.

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

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

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

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

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

North East Scotland Biological Records Centre, 2017. NE Scotland mollusc records 1800-2010. Occurrence dataset: <https://doi.org/10.15468/qsluuv> accessed via GBIF.org on 2018-10-01.

OBIS (Ocean Biogeographic Information System), 2019. Global map of species distribution using gridded data. Available from: Ocean Biogeographic Information System. www.iobis.org. Accessed: 2019-03-04

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

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

South East Wales Biodiversity Records Centre, 2018. Dr Mary Gillham Archive Project. Occurrence dataset: <http://www.sewbrec.org.uk/> accessed via NBNAtlas.org on 2018-10-02

Suffolk Biodiversity Information Service., 2017. Suffolk Biodiversity Information Service (SBIS) Dataset. Occurrence dataset: <https://doi.org/10.15468/ab4vwo> accessed via GBIF.org on 2018-10-02.