Mass mortalities in bivalve populations: A review of the edible cockle *Cerastoderma edule* (L.)

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Abstract

Mass mortalities in bivalve populations have long been of particular concern, especially when the species supports a commercial fishery or is of conservation interest. Here we consider the evidence of mass mortalities of the edible cockle, *Cerastoderma edule* (L.). Through the construction of a conceptual model eight potential factors (or groups of factors) which may cause mass mortalities are identified and reviewed. These include: food limitation; density; oxygen depletion and organic loadings; temperature and salinity; parasites, pathogens and commensals; toxicants and other persistent pollutants; predation, and changes in sediment, suspended solids, topography and bathymetry. The interplay between factors in recognized and discussed based on evidence mainly from the published literature relating to temperate edible cockle beds. Anecdotal evidence is also reported from a structured survey of site-specific evidence provided by fisheries managers in England and Wales. Case studies from the UK and Europe indicate that there is often no single, clear generic cause of mass mortalities in cockle populations. The importance of linked site-specific scientific investigations and laboratory-based experiments to fill the gaps in our current understanding of mass mortalities in bivalve species is highlighted as necessary to take account of both local extrinsic and intrinsic factors.

Keywords: mass mortalities; bivalve populations; conceptual model; *Cerastoderma edule*; edible cockle, shellfisheries management

1. Introduction

All natural bivalve populations suffer mass mortalities (Orton, 1933; Jonsson and Andre, 1992; Wootton et al., 2003) and although there is a wealth of anecdotal evidence to support this, such events are not always published in the scientific literature. It is clear from studies of mortality events that it is difficult to unequivocally assign a cause to the deaths (Malham et al., 2012; Callaway et al., 2013). Often it is not possible to determine the relative influences of each cause on total mortality, and indeed whether some are causes or merely symptoms of the problems observed. Therefore, there is the need for scientifically rigorous reviews of the possible factors which cause mass mortalities in bivalve species. Such mass mortalities are of particular concern when the species either supports a commercial fishery or is of nature conservation importance, for example as an important food resource for protected wading birds (Parada and Molares, 2008; Callaway et al., 2013). As such an improved understanding of possible causes of such episodic mass mortality events will aid in the management of both commercial fisheries and nature conservation.

The focus of this review is the edible cockle, *Cerastoderma edule* (L.). *C. edule* lives in semi-sheltered, intertidal or shallow subtidal marine systems, and has a wide geographical distribution from Norway to Mauritania (Honkoop et al., 2008) and through the Baltic, Mediterranean and Black Sea (Longshaw and Malham, 2013). Cockles are suspension feeders, relying on phytoplankton and organic matter in the water column; they live just below the surface of the sediment and use short siphons to extract their food from just above the sediment-water interface. In the food chain, cockles are a link between primary producers (phytoplankton, phytobenthos) and consumers such as crabs, shrimps, fish and birds (Reise, 1985). Malham et al. (2012) recently reviewed the biology of *C. edule*, including its genetics, reproduction and development, energy and growth, and immunology.

With respect to reproduction and development, *Cerastoderma* species generally undergo gametogenesis in February/March followed by rapid gonadal development in April and May before spawning around May to July/August (Malham et al., 2012). Their eggs are pelagic and develop in the plankton for three to five weeks before settling on the sediment as spat at a size of approximately 280 mm shell length (De Montaudouin and Bachelet, 1996). High rates of mortality are naturally observed during these early life history stages (Rodriguez et al., 1993). From then on, cockles are benthic organisms, and their survival and subsequent recruitment into the adult population can be influenced by several intrinsic physiological factors such as disease and poor body condition, and extrinsic factors such as climate change and removal by predators (Longshaw and Malham, 2013; Callaway et al., 2013) and can result in a gradual decline in cockle population numbers over time. However, there has been an increase in cases of unexplained episodic mass mortality events in European cockle populations (Malham et al., 2012). The difficulty in distinguishing between natural mortalities and unnatural episodic mass mortality events has been recognized (Callaway et al., 2013). This review focusses on episodic mass mortality events which occur over a relatively short time period; natural mortality events which often occur over longer periods and affect earlier life stages are not included here.

Mass mortalities of *Cerastoderma edule* (L.) populations, have been sporadically reported for over a century, with reports on the Lancashire coast (UK) dating from 1904 (Scott, 1910). Large numbers of mass mortality events of *C. edule* have also been reported from across Europe, including in the UK, Netherlands, France, Portugal, Spain and Sweden (Malham et al., 2012). Most reports of mass mortality are from monitored, commercially exploited shellfishery beds, while mortalities of non-commercial stocks are often under-reported. In the UK, for example, several fisheries management authorities have recorded mortalities of *C. edule* but most of these mass mortality events remain unexplained, or with only anecdotal evidence to suggest possible causes (Table 1). This evidence from 16 sites in England and Wales shows that cockle mortalities have long been occurring, from the Solway on the NW coast of England south to the SW coast of Wales, and on the east coast of England from Budle Bay in Northumberland south to The Wash (Fig.1). Although causes for such mass mortalities have been suggested by the fisheries management authorities, there have been very few cases identified in the UK, or elsewhere, where detailed studies have been carried out to explore the background of the problem.

Here we identify and review a number of factors that are known, or are suspected, to cause episodic mass mortalities in cockle populations. The construction of a conceptual model provides a framework to capture the key intrinsic and extrinsic factors which may contribute

towards, or cause mass mortalities in cockles. This framework not only provides a structure for the review but provides a suitable guide for future holistic site-specific studies of mass mortalities in bivalve species. The response of cockles to individual factors is explored, and the likelihood of these factors leading to mass mortalities is assessed based on the published evidence. The importance of interplay between the individual factors is also discussed. The anecdotal evidence proved useful in identifying potential gaps in our understanding and highlighted areas where future research may be required. Although the focus of this review is on one particular bivalve species (*Cerastoderma edule*), several of the factors and therefore lessons learned may apply to other benthic bivalves.

Table 1: Incidences of cockle mortalities in England and Wales reported before July 2013. Information collated from the Inshore Fisheries and Conservation Authorities and Environment Agency regional staff. See Fig. 1 for site locations.

Geographical area	Reported mortality events	Suggested causes
Solway Firth North (SW Scotland), South (NW England)	Cockle mortalities reported mainly from the north side of the Firth (c. 2005–2011).	Fishing, instability of beds (washing out).
Morecambe Bay (NW England)	Mortalities reported through the bay since c. 2005. Mainly loss of spat and some mortalities of older year classes.	Cold winters, instability of beds (washing out).
Ribble Estuary (NW England)	Mortalities, particularly of spat (since 2005). Always a cyclical fishery and showing encouraging signs for 2014.	Strong hydrodynamic forces are mainly held responsible; other factors unknown.
Wirral (NW England)	Collapse of stock in autumn/winter after high spatfall (late 1990s). Further mortalities reported in 2010. Poor stocks with only a limited fishery in 2013, although with some very dense patches.	Oystercatcher predation, fisheries.
Dee (N. Wales), West Kirby (Wirral)	Mortalities of >1 year old cockles (June 2009).	Barnacle infestation wedges cockle shells open, high temperatures, high algal production, settlement of mussels on cockle shells.
Dee (general) (N. Wales)	Loss of traditional cockle harvesting areas (2010 to date). Cockles have moved into new areas of the estuary over the same period.	A generally healthy cockle population threatened in some areas by an invasion of mussels which change the substrate making it unfavourable for cockles.
Traeth Lafan (N. Wales)	Mortalities of adult cockles in high density parts of the bed (July and August 2008–2009). In 2013, the fishery was considered to be healthy and as good as any in the past.	High cockle density.
Dyfi (Dovey) (Mid Wales)	Mortalities reported in 2001 and 2008.	No cause(s) suggested.
East Angle, Pembroke Dock (S. Wales)	Localised mortalities of larger cockles, mostly in June and July (since 2005). Episodic events.	No cause(s) suggested.
Three Rivers Estuary (S. Wales)	Localised mortalities reported since 2003. Some recent improvement with guarded optimism for the future.	No cause(s) suggested, but generally similar to Burry Inlet.
Burry Inlet and Loughor estuary (S. Wales)	All areas affected by mortalities of 1-winter and older cockles. Protracted mortalities particularly in spring and summer months. Records of mortalities since 2003. Some signs of better survival of 2 + year class in 2013.	High parasite loading, high densities, post-spawning mortality.
Fal Estuary (SW England)	Mortalities reported in August 2008, July 2009, and September 2010.	Parasites were investigated, but causes largely unknown.
Helford River, West Penwith (SW England)	Large numbers of mortalities reported in August 2008.	Parasites, virus.
Camel Estuary, Town Bar (SW England)	Poor cockle stocks despite high spatfall, mortalities of older cockles in summer (2008–2011). Reduced biomass in 2012 but good survival in 2013.	Harsh winter conditions, similar mortality pattern as in Burry Inlet.
The Wash (E. England)	Cockle mortalities particularly amongst the 1year class reported in (2000, 2008–2011). Mortality continues particularly during post-spawning and after warm periods.	Competition between cohorts, carrying capacity may be exceeded, parasites.
Horseshoe Point, Cleethorpes (E. England)	Protracted cockle mortalities similar to the Burry Inlet (2010/2011). Atypical mortalities continued in 2013.	No causes suggested.
Budle Bay (NE England)	High mortalities of 1 winter and older cockles reported (summer months of 2008–2009).	Phosphate stripping in sewerage treatment works, opportunistic algae.

Figure 1: Location of cockle mortalities in England and Wales (details provided in Table 1).

2. Factors affecting cockle mortalities

Owing to high natural variability in recruitment success and survival rates in cockles it can be difficult to differentiate between natural mortality and unusual die-offs (Parada and Molares, 2008). In an attempt to better understand the possible causes of mass mortality events, a conceptual model was developed which highlights the important links and provides the causes and consequences of change in cockle populations and the possible causes of mass mortalities (Fig. 2). This model is not designed to illustrate socio-economic consequences nor the solutions to any problems identified. These issues are considered outside the scope of the current review.

Cockle mortality can be the result of external (extrinsic) factors, including both physico-chemical and biotic factors, such as competition for food and space, poor environmental quality, or removal by predators. Internal (intrinsic) physiological factors may also play a part and include the effects of disease, poor body condition and post-spawning mortality. Both the extrinsic and intrinsic factors which may affect cockle health and survival have been highlighted (Fig. 2). The model is designed as an initial assessment of the possible key factors which may cause mass mortalities of the edible cockle and illustrates potential linkages between factors (highlighted using double-headed arrows).

In general, eight key factors (or groups of factors) have been identified as potentially causing mass mortalities in cockle populations. Each of these factors will be reviewed in turn. They include: food limitation; density; oxygen depletion and organic loadings; temperature and salinity; parasites, pathogens and commensals; toxicants and other persistent pollutants;

predation, and changes in sediment, suspended solids, topography and bathymetry. It is recognized that some of the factors identified by the model may cause natural mortalities within cockle populations, either as a result of poor body condition, the age of the cockle bed or post-spawning mortality. However this review will only focus on the factors which have the potential to cause episodic mass mortalities in cockle populations.

2.1. Food limitation

Cockles are shallow burrowing organisms, which live in intertidal or shallow subtidal areas, and use their short siphons for filter feeding phytoplankton from the water column (Ansell et al., 1981; De Montaudouin, 1996). Their food supply is determined by three main factors: the concentration of food particles in the water, the current velocity of the water, and immersion period (Kamermans, 1993). Potential relationships have been identified between feeding time (immersion) and the quantity and quality of food available (Fig. 2). These factors may have the potential to cause mass mortalities in cockles, for example, a significant reduction in immersion time (as a result of natural or anthropogenic changes and due to the cockles occurring at higher intertidal levels) reduces growth rates and therefore the survival of the cockles (Elliott, 1979). Kamermans (1993) investigated food limitation in cockles, as a result of low phytoplankton concentrations and low current velocity in the Wadden Sea, and reported that both of these factors have a negative effect on the growth of *Cerastoderma edule* although no link to mass mortality was found. De Montaudouin (1996) studied the growth of C. edule in Arcachon Bay, southwest France, and proposed a threshold for immersion (70%) above which net growth is null and consequently life span must be reduced.

The importance of food limitation in cockles has been studied in relation to growth (Kamermans, 1993; De Montaudouin, 1996) although there is no specific published or anecdotal evidence which directly links food limitation to mass mortality in cockle populations. Given the highly productive nature of estuarine environments (McLusky and Elliott, 2004), it is unlikely that food limitation would cause mass mortalities within cockle beds and therefore at present this factor is considered unlikely to be a cause. The interplay between food limitation and density is recognized by the model (Fig. 2) and is further discussed below.

2.2. Density

Density has been described by many authors as being one of the factors that could affect both the growth and mortality of cockles (and other bivalves) in relation to intraspecific competition (for food and space) and the incidence of predators (De Montaudouin and Bachelet, 1996). Malham et al. (2012), for example, also recognizes that population success in cockles can be negatively influenced by both inter and intra-specific competition, particularly in relation to growth and density. Cockle population dynamics undergo natural cycles, governed by periods where cockle densities collapse, phases of recovery and more constant phases where higher densities of cockles are maintained within the bed; the duration of these cycles can vary between one and ten years (Ducrotoy et al., 1991). Densities fluctuate greatly, and while individual cockles can live for up to 13 years, the turnover in some areas is fast and cockles may only just reach their second year (Dörjes et al., 1986; Ducrotoy et al., 1991; Genelt-Yanovskiy et al., 2010; Gam et al., 2010). Where cockles occur in high densities, density-dependence and the influence of this on mass mortalities should be considered, for example whether they suffer from competition for food and/or space. This factor is therefore closely

linked to food limitation (Fig. 2). Whereas deposit, detritus and predatory feeders are all limited by food availability, suspension feeders such as cockles are usually limited by space (Levinton, 1972; Gray and Elliott, 2009). Richardson et al. (1985) described the influence of density on competition for space, suggesting that collisions between individuals in close proximity cause the animals to emerge at the sediment surface, which makes them more vulnerable to predators and more susceptible to hydrographic conditions.
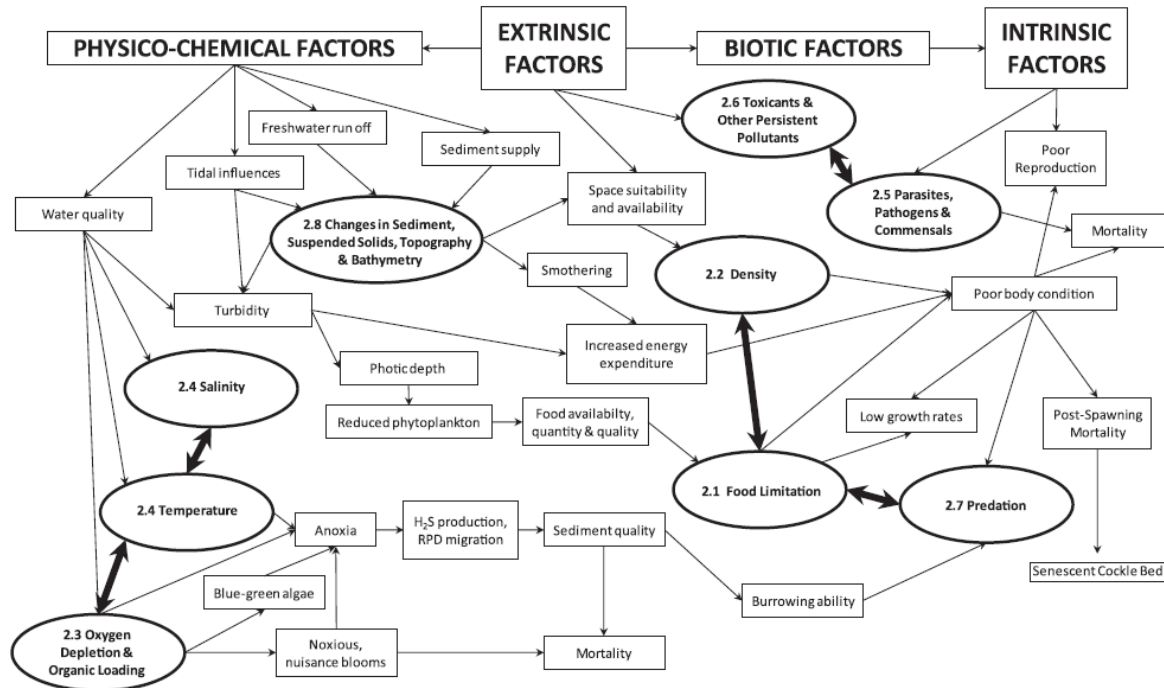

Figure 2: Conceptual model of the possible causes of mass mortalities in cockles. The key factors included within this review are circled and include their respective section numbers. Thick double-headed arrows represent potential interplay between key factors.

High densities of cockles potentially have a lower growth rate. In the Wadden Sea (Denmark), the size of cockles at a high density with over 2,500 cockles m^2 was considerably smaller than those from less densely populated sites in the same area (Jensen, 1992). There was no reported evidence to suggest that such lowered growth rates could be a direct cause of mass mortalities within cockles. De Montaudouin and Bachelet (1996) manipulated low and high population densities (160-2000 adults m^2) and tidal elevations (low- and mid-water levels) of *Cerastoderma edule* inside field enclosures at Arcachon Bay, SW France to test the influence of both adult densities and emersion time on growth, settlement and survival. Although growth rates were affected by both tidal height (higher growth rates at low water level) and density (decreasing growth rates as density increased up to a point after which it remained constant), no mass mortality was observed.

A recent study investigating high cockle mortalities from two sites within the Burry Inlet (South Wales, UK) suggests that density may be a cause of stress given the significant/high strength of the correlation between cockle density, cockle size and mortality rate (Elliott et al., 2012). This was further investigated by Callaway et al. (2013) who compared mortality rates at two sites on the south side of the Burry Inlet, one high density site (1141 ± 116 cockles m^2 for 1-

year olds) and one low density site where the cockle population was approximately half as dense. This study showed that there was no significant difference between mortality rates at each of the Burry Inlet sites and concluded that high densities were not a principal cause of the cockle mortalities.

Parada and Molares (2008) analysed the relationship between cockle mortality and the population density, precipitation and atmospheric temperature during a seven year period in the Ria of Arousa, NW Spain. They suggest that density levels may cause mass mortality as a result of intra-specific competition for food and space and the incidence of predators (after De Montaudouin and Bachelet, 1996). Their study of modelled data showed that mortality of cockles in two adjacent bays increases with population density and this relationship follows a sigmoidal function implying that mortality of cockles within the Ria of Arousa is density-dependent and increases when density is >500-600 individuals m^2. Anecdotal evidence from The Wash, eastern England, suggests that recent mass mortalities in cockle populations may have been the result of competition between cohorts, with the 1-year class mainly being affected, and that the carrying capacity of the fishery may have been exceeded (see Table 1; Fig. 1), although no further explanation was provided. There were also mortalities reported of adult cockles in high density parts of the cockle beds at Traeth Lafan (North Wales) between July and August 2008-2009, although recent evidence suggests the beds are now showing signs of recovery (see Table 1). Inter- and intra-specific competition for food may be an important issue in relation to the growth of cockles and other bivalves, but there is insufficient evidence to relate competition for food to high mortality rates in cockles. This requires further investigation.

2.3. Oxygen depletion and organic loadings

Domestic sewage and agricultural run-off are the major sources of nutrients and dissolved and particulate organic matter to estuarine and coastal waters (Gray et al., 2002). Increased nutrient loadings in the water may lead to several signs and symptoms of eutrophication, one of which is benthic mortalities (Elliott and de Jonge, 2002). Linked to this is a reduction in oxygen content, potentially leading to anoxia within the water and the sediment, which will have a major influence on cockles and other benthic fauna. Insufficient oxygen in the water column will cause direct mortalities whereas a lack of oxygen in the bed will cause the redox potential discontinuity layer, the aerobic-anaerobic separation, to migrate towards the surface. This leads to the development of opportunistic macrobenthic populations and thus changes along the Pearson-Rosenberg continuum (Fig. 3) (Gray and Elliott, 2009). When hypoxic conditions occur, mobile organisms will try to leave the area, however sessile organisms and infauna will suffer mortalities. This will occur first in the more sensitive crustaceans and echinoids, followed by bivalve molluscs and then lastly by the more tolerant annelids (Gray et al., 2002) (Table 2).

A cockle population collapse in the Bay of Somme (north France) during the period 1982e1985 was attributed to eutrophication and the induction of anoxia (Desprez et al., 1992; Rybarczyk et al., 1996). Changes to the benthic community were summarized as an observed rapid increase in the density of the spionid worm *Pygospio elegans* in the absence of *Cerastoderma edule*, but an almost complete disappearance of that species once the cockles returned.

Evidence from the 1980s from Laholm Bay, western Sweden, suggested a correlation between increased nutrient levels and observed mass mortalities of *Cerastoderma edule*, although no direct causal link was established (Rosenberg and Loo, 1988). Their study

proposed that increased nutrient levels leading to eutrophication may contribute indirectly to mass mortalities in *C. edule* populations, and it may be the resultant reduction in oxygen which may be the more important factor.
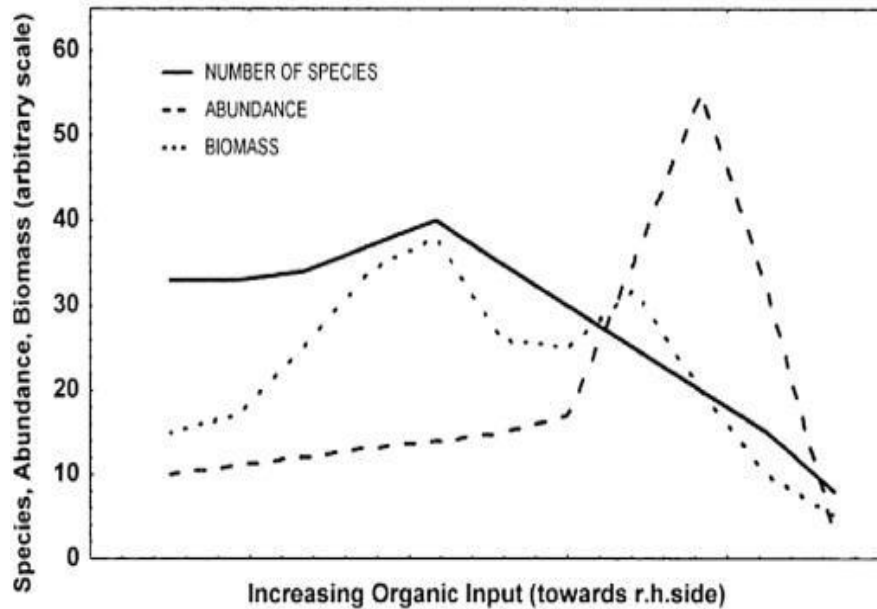

Figure 3: The Pearson Rosenberg model showing species, abundance and biomass curves of the effects of organic enrichment on sediment-living organisms (Gray et al., 2002).

Table 2: Summary of the effects of reduced oxygen concentrations on marine organisms (Gray et al., 2002).

Type of organism	Effect	Concentration (mg L^{-1})
Actively swimming fish	Growth	6
Actively swimming fish	Metabolism	4.5
Bottom-living fish	Metabolism	4
Most fishes	Mortality	2
Crabs, shrimps, lobsters	Growth	2–3.5
Bottom living isopods	Mortality	1–1.6
Bivalve molluscs	Growth	1–1.5
Annelids	Growth	1–2
Mudskipper	Mortality	1

In Portugal, 10,000 ha of the Ria Formosa are used for extensive clam culture (including the edible cockle *Cerastoderma edule* and other bivalve species). Recent mass mortalities of shellfish of up to 50% have been observed within the Ria Formosa and these have been related to sewage discharges at Olhão (Mudge and Bebianno, 1997), although the specific impact on *C. edule* alone was not reported.

In the Burry Inlet, sewage discharges were alleged by the local cockle fishermen as the most likely cause of the observed mass mortalities in cockles. In response, Elliott et al. (2012) investigated the potential changes in benthic communities in relation to the observed annual cockle mortalities in the Burry Inlet (South Wales). There was no observed change in the

benthic community during the study period and therefore water quality, including oxygen and organic loadings, was excluded as a possible factor for the observed mortalities. This was further demonstrated by Callaway et al. (2013) who showed that there was no significant change in the populations of the Baltic tellin bivalve (*Macoma balthica*) and the spionid polychaete (*Pygospio elegans*) in relation to the high cockle mortalities observed in the Burry Inlet. Their study did, however, show a significant relationship between declining cockle numbers and an increase in the number of other benthic individuals suggesting that the cause of cockle mortalities was species-specific.

Hence sufficient evidence from several studies generally suggests that oxygen depletion and organic loadings may be a likely cause of mass cockle mortalities, but this would only be so if there were concomitant changes in the remainder of the benthic assemblage (Gray and Elliott, 2009). In the Burry Inlet oxygen depletion and organic loading was discounted as a likely cause of cockle mortalities as the benthic community showed no evidence of any change that could be related to the factors. These findings emphasize the importance of site-specific monitoring to assess a number of potential causes of mass mortalities, given the highly dynamic nature of the estuarine environment.

2.4. Temperature and salinity

All organisms live within a set of tolerances for each environmental variable, such as temperature and salinity, and if those variables increase or decrease outside the tolerance levels then the organisms will suffer adverse effects (e.g. Wither et al., 2012). For example, most marine invertebrates have temperature thresholds that initiate maturation and spawning (Rasmussen, 1973), and so elevated or lowered temperatures have the potential to delay or initiate spawning, which may have severe knock-on effects on the population dynamics.

2.4.1. Low temperature

Mass mortalities in cockle populations have been reported as a result of low ambient temperatures. For example, Kristensen (1958) found in the Wadden Sea during a severe winter in 1954 that the sediment froze to a depth of 10-15 cm resulting in mass mortalities of *Cerastoderma edule*. Crisp (1964) reported several studies on the effects of the severe winter of 1962/63 on the marine life in Britain with some of these studies specifically relating to mass mortalities of *C. edule*. Hancock and Urquhart (1964) observed almost total mortalities of cockles in Llanrhidian Sands (Burry Inlet, South Wales) following the harsh winter of 1962/63 and also mass mortalities in other areas around the UK including Morecambe Bay, Shoeburyness and Whitstable. During the same harsh winter period, Waugh (1964) reported mass mortalities on native oyster (*Ostrea edulis*) beds and the associated fauna (which included *C. edule*) in southern England, whilst Perkins and Williams (1964) observed mass mortalities in *C. edule* populations in the Solway Firth, caused directly through ice formation on the upper shore and indirectly from predation by oystercatchers and gulls as, cockles provided the only food source available to them. Beukema (1979) describes the effect of low temperatures on macrobenthic community structure in the western Wadden Sea during a severe winter in 1979. Declines in *C. edule* were observed due to the low temperatures, with other bivalves such as *Abra tenuis*, *Angulus tenuis* and *Mysella bidentata* also being affected.

2.4.2. High temperature

High temperatures can also cause mass mortality of bivalve species, but since thermal tolerances of the common estuarine species are fairly similar it is expected that observations would include multiple species (Compton et al., 2007; Wither et al., 2012). In addition, synergistic effects can occur, such as the presence of organic matter coupled with higher temperatures, which will influence oxygen levels in the water and sediment (Fig. 2). For example, mortality in juvenile cockles due to high temperatures has been reported in Arcachon Bay (Bachelet, pers. comm. in Guillou and Tartu, 1994) and Galicia (Gonzalez and Perez Camacho, 1984) although these mass mortalities were probably the result of anoxia (Guillou and Tartu, 1994). This again demonstrates the interplay between factors such as temperature and oxygen depletion and organic loading as highlighted by the conceptual model (Fig. 2) and as such these factors require to be investigated together.

2.4.3. Salinity

In the Baltic Sea, for example, cockles have been reported to tolerate salinities as low as 10-11 (Brock, 1980), although they also survive in near full-strength sea water (Kingston, 1974). A modelled study in the Western Scheldt found that cockles would thrive in salinities between 10 and 30, although the optimum salinity for the species was 25 (Ysebaert et al., 2002). Laboratory studies showed that *Cerastoderma edule* larvae have a salinity preference of between 30 and 35, but can survive in salinities as low as 5 (Kingston, 1974). Despite the wide salinity range tolerated by the cockle, Kristensen (1958) suggested that mass mortality associated with heavy rainfall events (thus reducing salinity within the water column and sediments) is a common occurrence. No further evidence was found which directly linked changes in salinity to mass mortalities in *C. edule*.

As indicated above, extreme lows of temperature, particularly during harsh winters, have been associated with mass mortalities in cockles, but extremely low salinity could possibly also affect mortality rates. Synergistic effects of high temperature and low oxygen levels may also be important but as yet there are no data on the energetic repercussions of tolerating such extremes of these environmental factors.

2.5. Parasites, pathogens and commensals

A wide range of parasites, pathogens and commensals do affect the individual and population health of cockles, although there is currently a lack of understanding of the link between infestation and mass mortalities (Longshaw and Malham, 2013). It is considered likely that the impact of parasites, pathogens and commensals can indirectly contribute to mass mortalities by either weakening individuals, or infecting individuals which have already been stressed by another factor or a combination of factors. Jonsson and André (1992) investigated the mass mortality of *Cerastoderma edule* during the summer of 1991 in Scandinavian waters and concluded that the infestation intensity and tissue damage together with field observations strongly indicate that infestation by the trematode parasite *Cercaria cerastodermae* I impaired the burrowing ability of the individuals and thus was the likely cause of the mass mortality. Blanchet et al. (2003) investigated the effects of digenean trematodes and heterotrophic bacteria on the mortality and burying ability of *C. edule* in Arcachon Bay, SW France. Based on both field observations and laboratory experiments, Blanchet et al. (2003) suggest that bacteria, rather than digenean trematodes, could play a role in the emergence of cockles, and, hence affect their survival in the wild. Thieltges (2006) investigated a conspicuous cockle mortality in the northern Wadden Sea in the late summer of 2004. A combination of field sampling and

laboratory experiments suggested that trematode parasites such as *Gymnophallus choledochus* may act as a castrating agent and thus should be considered as a likely mortality factor in adult cockle populations.

Longshaw and Malham (2013) recently reviewed parasites, pathogens and commensals of European cockles, which included those affecting *Cerastoderma edule*. Their review highlights a total of 50 different agents being reported, including viruses, bacteria, fungi (including Microsporidia), Apicomplexa, Amoeba, Ciliophora, Perkinsozoa, Haplosporidia, Cercozoa, Turbellaria, Digenea, Cestoda, Nematoda, Crustacea and Nemertea.

In the Burry Inlet (South Wales), there was an observed increase in the number of parasites present within cockles observed between 1999 and 2009 (Elliott et al., 2012). The study concluded that it was not possible to determine whether the parasitism caused or contributed significantly to the observed mortalities.

The literature therefore suggests that parasites and diseases can contribute to mortalities in adult cockle populations, however it is currently unclear whether this factor is a direct cause of episodic mass mortalities. There are gaps in our current understanding and a greater level of understanding is needed particularly on the life-cycles of such mortality drivers (Longshaw and Malham, 2013).

2.6. Toxicants and other persistent pollutants

Marine bivalve molluscs, including cockles, are well known to be sensitive to a wide variety of direct toxicants found in the marine environment. Toxicants may influence the increasing disease incidences reported in marine animals, possibly by inducing immunosuppression that in turn would severely compromise defence against parasites and pathogens (Wootton et al., 2003). This highlights the potential interplay between toxicants and pathogens, parasites and commensals (see Fig. 2). With respect to degradable waste, mass mortalities of *Cerastoderma edule* were observed after a major oil spill, following the grounding of the Sea Empress in 1996 off the SW coast of Wales (SEEEC, 1998). Similar mortalities were also observed in other bivalve molluscs, for example the razor-shell (*Ensis siliqua*); however, the marine mussel *Mytilus edulis* underwent significant immunosuppression but did not show oil-induced mortalities. Wootton et al. (2003) investigated the impact of oil and hydrocarbons (polycyclic aromatic hydrocarbons, PAH) on the immune cells and functions of the same three closely related species (*C. edule*, *E. siliqua* and *M. edulis*) and demonstrated that the immune cells and functions differed extensively in response to oil, with *M. edulis* showing a much higher level of immunological vigour. Their laboratory-based study also showed that all three species showed a different immunological response to exposure to PAH, with *C. edule* being the most sensitive species. Despite this finding, there is no evidence to suggest that exposure to hydrocarbons has been the direct cause of mass mortality on any natural cockle beds.

Among pollutants, heavy metals are dominant contaminants in marine and estuarine environments and represent an increasing area of concern within environmental fields. Jenner and Bowmer (1990) investigated the accumulation of heavy metals compounded by the associated biological effects on *Cerastoderma edule* of Pulverised Fuel Ash (PFA), a by-product of coal-fired power stations. Their study, based on mesocosm experiments, demonstrated that intermittent exposure to PFA resulted in mass mortalities of C. edule. Their evidence from

studying *C. edule* and two other benthic species (*Arenicola marina* and *Mytilus edulis*) led to the conclusion that dumping of PFA as ash in a marine environment will lead to severe depletion of the invertebrate populations in situ, with metal accumulation in the benthic fauna. Despite the inherent effects of fine particles, such as PFA, on the gills of suspension feeders, no site-specific incidences of high cockle mortalities, as a direct result of PFA deposition, have been identified within the literature.

Although toxicants and other persistent pollutants can adversely affect marine organisms, there is limited evidence relating to them being a direct cause of mass mortalities in cockles. There is a wider literature available for example regarding the physiological impacts of toxicants and other persistent pollutants (see for example Wootton et al., 2003), although these studies are based upon laboratory experiments with no site-specific evidence obtained to link such impacts to mass mortality events on natural cockle beds.

2.7. Predation

Cockle predators include wading birds, intertidal feeding fish and crustaceans such as shore crabs and shrimps, with different species targeting specific sizes of cockle (see Fig. 4). Juvenile cockles below 11 mm in length have been shown to be targeted in the Bay of Morlaix, France, and predation was responsible for 85% of their mortality (Masski and Guillou, 1999). Möller and Rosenberg (1983) reported that predation by the brown shrimp *Crangon crangon* on juvenile cockles in Sweden removed 68% of the production of *C edule* in one year. These studies indicate that the survival of *C. edule* is density and size dependent, with the effect of predation being reduced by high recruitment and rapid growth beyond the critical size for being captured.

Predation of cockles by oystercatchers resulting in mass mortalities has been observed in the Wadden Sea by Jensen (1992) and Beukema (1993). However, these studies also suggested other factors such as overfishing as potential causes. Ducrotoy et al. (1991) proposed that predation from birds is less important as a factor controlling overall cockle densities than other factors, such as severe winters, parasites or post-spawning mortality.
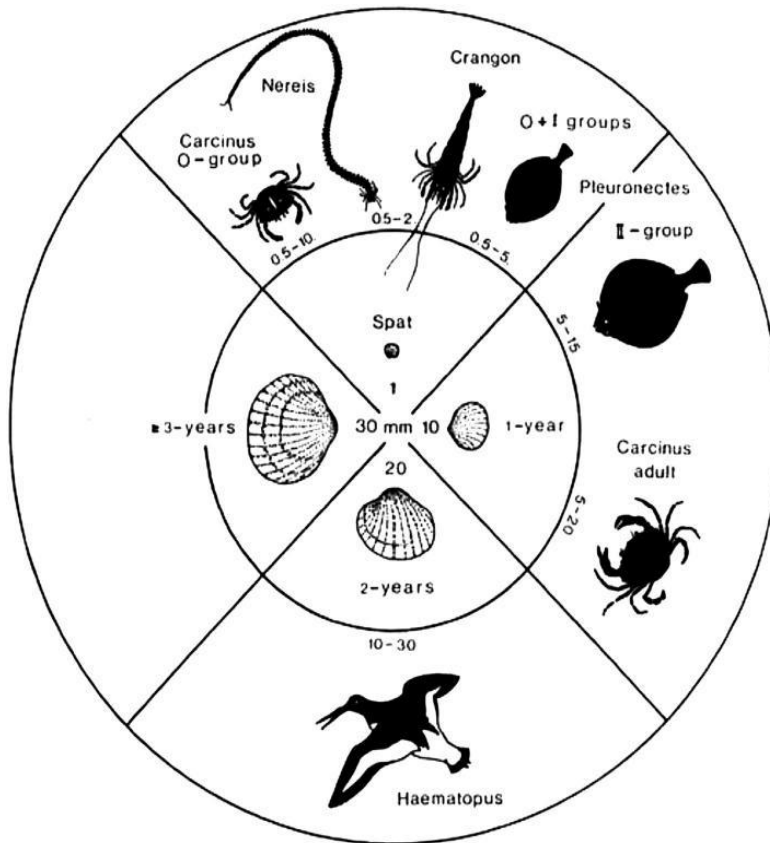
Figure 4: Predator spectrum of the cockle Cerastoderma edule growing from spat to adult size. Prey spectrum given in shell length (mm) in the inner circle (after Reise, 1985).

Sanchez-Salazar et al. (1987) investigated the interactive role of tidal elevation and predation with respect to cockle populations at Traeth Melynog, North Wales. Their study showed that in low shore areas, up to 96% of cockle spat did not survive their first summer, but mortality rates subsequently declined and remained at a low level thereafter. In contrast, cockles found high on the shore suffered moderate mortality during their first year (47%), but mortality rates subsequently increased. The study concluded that these contrasting patterns of mortality were related to predation, with shore crabs preying on juvenile cockles on the lower shore until they reach a certain size, and oystercatchers predating adult cockles in the upper shore regions.

In general, predation by shore crabs and brown shrimp has mainly been reported as a factor affecting the survival of juvenile cockles on the lower shore whilst oystercatchers are reported as being the main predator of adult cockles in the upper shore. It is likely that predation will lead to a gradual decrease in cockle numbers, potentially resulting in high mortalities over a longer period, however it is unlikely that predation would result in an episodic mass mortality event as discussed in this review.

2.8. Sediment, suspended solids, topographic and bathymetric change

Cockles have a preference for non-extreme tidal heights (Beukema and Dekker, 2009), and type of substratum, usually muddy sands and sands in the mid-low shore areas (Wolff, 1973; Rasmussen, 1973; Elliott, 1979). An increase in sediment accretion could lead to smothering together with the animals being raised in the intertidal area to a tidal height away from their

optimum. The latter will result in reduced emersion times and thus be associated with food limitation. Elliott et al. (2012) recognized that some accretion by sediment occurred in the Burry Inlet, South Wales, as part of a wider study into cockle mortalities. However, it was not known whether this was sufficient to raise the cockles to higher and less optimal tidal levels and thus cause stress to them; given the normal environmental tolerances of cockle populations, this was deemed unlikely. Conversely, excessive erosion could lead to the animals becoming uncovered and thus away from any buffering effects of the sediment, subjecting them to surface conditions, temperature extremes and predation (see Fig. 2).

Changes to the local hydrographic regime as a result of anthropogenic activity or extreme events, for example a storm, will change the sediment type and can negatively impact suspension and deposit feeders through clogging of feeding structures due to high turbidity and smothering (Norkko et al., 2002). 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. Anecdotal evidence from the Ribble Estuary, NW England suggests that mass mortalities in local cockle populations are a result of strong hydrodynamic forces (Table 1; Fig. 1). In addition the instability of the beds was proposed as a cause of mass mortalities of cockles in Morecambe Bay and in the Solway Firth (Table 1; Fig. 1).

Apart from the study of Gam et al. (2010), there is no further published evidence available to suggest that sediment, suspended solids and/or topographic and bathymetric change has been the cause of mass mortality events in cockles. Anecdotal evidence suggests that instability of the beds and strong hydrodynamic forces may be possible factors to consider when assessing potential impacts on mass mortalities in cockle, although further scientific investigations would be required.

3. Final discussion and conclusions

This review has focussed on episodic mass mortality events which effect large numbers of the *Cerastoderma edule* population over a relatively short period. Eight potential causes of such mass mortalities events in *C. edule* were reviewed, although within the literature no single, clear generic cause of mass mortalities in cockles was identified. Evidence was gathered from the published literature and focused mainly on case studies from the UK and elsewhere in Europe. Overall, evidence was relatively limited with most studies focusing on a particular pathway through the conceptual model; very few studies have taken a wider holistic approach, recognising the importance of the linkages between the various pathways and also linkages between mass mortality factors.

In addition to the published literature, anecdotal evidence was collated from fisheries managers within England and Wales. This evidence was obtained by face-to-face meetings or via in-depth telephone conversations with fisheries managers who work directly with stock assessments of cockle beds within their jurisdiction. The anecdotal evidence provided suggests that mass mortalities in *Cerastoderma edule* have occurred throughout most UK coastlines, with possible causes for the observed mass mortalities being put forward by the respective fisheries managers. The reporting of this anecdotal evidence allows for direct

comparisons between the spatial and temporal occurrences of mass mortality events and opens up such data for the first time to the wider scientific community. The anecdotal evidence underpins this review and assisted in identifying potential gaps in our understanding.

This review has attempted to assess the likelihood of eight factors (or groups of factors) in terms of their potential to be a direct cause of unexplained mass mortalities on beds of the edible cockle *Cerastoderma edule* based upon peer-reviewed evidence. For several factors there was insufficient published evidence to draw firm conclusions. Evidence from the literature highlights a few factors which have been directly linked to causing mass mortalities in cockles, for example harsh winters in the Wadden Sea and the Burry Inlet, and predation on juvenile cockles in Morlaix Bay, France. Partial evidence is available which suggests that a number of factors are considered as probable causes of mass mortalities, including cockle densities and the presence of parasites, pathogens and commensals, however the need for further studies into these factors is raised. Whilst many factors have been considered unlikely to directly cause mass mortalities in cockles, there was often no or limited evidence available to assess the potential impact of these factors. The review also recognizes the importance of interrelationships between various factors, hence the need to consider both synergistic and antagonistic effects. There may be several causes of mass mortalities in cockles and the cause(s) of the initial trigger may differ from the cause(s) of the continuing mortalities.

It is as yet unknown whether the number of mass mortality events in cockle populations is increasing on large spatial scales and may therefore signal wide-ranging changes in the population dynamics of this species, or whether the mortalities are local events caused by factors affecting individual cockle beds and discrete populations; this is an area requiring further study.

In coastal ecosystems, aquatic organisms undergo a variety of biotic and abiotic stressors that rarely occur independently. For example, a study by Paul-Pont et al. (2010) evaluated the interactive effects of cadmium contamination and pathogenic organisms (trematode *Himasthla elongata* and bacterium *Vibrio tapetis*) singularly and in combination during seven days on *Cerastoderma edule*. Their study highlighted the importance of considering the multiplicity of perturbation sources in coastal ecosystems to assess the health status of organisms. Results indicate that an interaction between pollutants and pathogens is much more complex than the direct single effects of pollution and parasitism alone, and cannot be deduced by simple addition.

This review emphasizes the site specificity of the evidence and thus the requirement for site-specific investigations supported by field and laboratory experiments in order to take into account local intrinsic and extrinsic factors. For example, the importance of site-specific evidence is apparent from the contrasting results presented on the impact of oxygen depletion and organic loadings on cockle mortalities in the Bay of Somme, France (Desprez et al., 1992; Rybarczyk et al., 1996) and the Burry Inlet, South Wales (Elliott et al., 2012; Callaway et al., 2013) respectively.

It was suggested by Malham et al. (2012) that routine cockle studies should obtain data on the following: length, age and growth, molecular samples to confirm species identity as well as population genetic stock, and the health and reproductive status of the population. Other measures such as density, estimates of mortality rates, associated fauna, sediment type,

salinity, temperature and water quality should also be taken. Given that there has not been a single factor identified which is responsible for all of the observed mass mortalities, then a holistic approach must be undertaken which will allow for an assessment of all pathways through the conceptual model presented here. One such example is the two-year study undertaken in the Burry Inlet, South Wales (Elliott et al., 2012), where literature surveys and a detailed field sampling and laboratory programme were initiated to holistically investigate a wide range of possible causes of the observed annual cockle mass mortalities. This study investigated multiple factors including the physical characteristics and water quality within the Burry Inlet, the ecology and dynamics of the benthos, cockle biology and health, and then linked the findings to fisheries and conservation management. It is recommended that a similar approach should be employed to investigate the factors responsible for the observed but unexplained mass mortalities of cockles highlighted by this review. Such an approach can also be applied to study mass mortality events of other bivalve species.

Acknowledgements

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