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A review of the biology of European cockles (*Cerastoderma* spp.)

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This review examines the biology of the two main cockle species Cerastoderma edule *and* C. glaucum *found in coastal areas around the north-east Atlantic from Norway to Morocco and through the Baltic, Mediterranean and Black Sea. It considers those factors in particular that impact on the overall health and survival of individuals as well as populations. Methods for the discrimination of the species are reviewed as well as the approaches being taken to delineate different populations, which is crucial to appropriately manage individual fisheries. Cockle populations generally undergo sexual maturation during their second summer and sexes are separate. Eggs are pelagic, with larvae being both benthic and pelagic before settling on the sediment and becoming benthic adults. However, data are lacking on basic larval biology and dispersal mechanisms. Data are provided on predator–prey relationships including information on types of food of importance to cockles. Main predators of cockles include brown shrimp, shore crabs, gastropods, polychaetes, fish and a variety of birds and these can be important in structuring cockle populations. Predation of larval cockles by adult cockles through larviphagy can lead to reductions of up to 40% of the population. Cockles are sensitive to a wide range of chemical contaminants but few data are published on impacts on cockles, in particular larval stages. The review concludes with an assessment of future climate change scenarios on cockles and considers some areas of future research required to preserve this ecologically and economically important species.*

Keywords: cockle, reproduction, genetics, predator, prey, chemical, immunology

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INTRODUCTION

This review considers factors influencing survival of the two extant species of cockle, *Cerastoderma edule* (L.) and *C. glaucum* (Bruguière, 1789) in European waters. Parasites, pathogens and commensals are treated separately by Longshaw & Malham (in press). The edible cockle *C. edule* is extensively exploited throughout its range and has a high economic value; its counterpart, the lagoon cockle *C. glaucum* is not commercially fished. Cockles are a bivalve occurring intertidally and subtidally around the coastline of Europe. *Cerastoderma glaucum* tends to occur in non-tidal areas such as lagoons and salt marshes whilst *C. edule* is more likely to be found on open coasts and in estuaries (Reise, 2003). They occur from Norway to Morocco and through the Baltic, Mediterranean and Black Seas. Although an overlap in distribution occurs at a large geographical scale for both species, *C. glaucum* is more common in the Mediterranean Sea and southern Europe and has been recorded from the coasts of Egypt, Tunisia, Turkey, Sardinia, Italy, Greece, Portugal, Spain, France (Atlantic and Mediterranean coasts), The Netherlands, the British Isles, Denmark, Finland, Norway and in the Wadden Sea, Baltic Sea, Mediterranean Sea, Black Sea, Adriatic Sea, Red Sea, Aegean Sea and Caspian Sea (Boyden, 1970; Ivell, 1979; Abdel-Malek & Ishak, 1980; Baudin, 1980; Labourg & Lasserre, 1980; Latypov *et al.*, 1995; Belofastova, 1996; Kevrekidis *et al.*, 1996; Amaral & Costa, 1999; Breber *et al.*, 2000; Carlsson, 2002; Erkan *et al.*, 2002; Reise, 2003; Arroyo *et al.*, 2006; Culurgioni *et al.*, 2006; Riisgård *et al.*, 2007; Derbali *et al.*, 2009b; Leontarakis *et al.*, 2009). On the other hand, *C. edule* is distributed along the north-eastern coastline of the Atlantic Ocean and into the Barents and Wadden Seas along the coasts of Norway, Sweden, Denmark, The Netherlands, Germany, the British Isles, France, Spain, Portugal and Morocco (Barnes, 1973; Seed & Brown, 1977; Wilson, 1980; Ivell, 1981; Armonies, 1992; Bachelet & Dauvin, 1993; Machado & Costa, 1994; Atkinson *et al.*, 2003; Flach, 2003; Bazairi *et al.*, 2005; Anajjar *et al.*, 2008; Cacabelos *et al.*, 2008; de Montaudouin *et al.*, 2009; Ponsero *et al.*, 2009; Andersen *et al.*, 2010; Genelt-Yanovskiy *et al.*, 2010). Longevity has been estimated to be in excess of 6 years for some populations, although with mortality events and poor growth, this can often be reduced to 2–3 years maximum (Jelesias & Navarro, 1990; Jensen, 1992; Lindegarth *et al.*, 1995). Population success can be negatively influenced by inter- and intra-specific competition, particularly in relation to growth and density (Jensen, 1992, 1993; de Montaudouin & Bachelet, 1996; Ramón, 1996)

Mortalities of cockles and catastrophic declines in cockle populations have been reported for many years with predation, disease, climatic events, pollution, failed recruitment and over-fishing being suggested as important factors (Ducrotoy *et al.*, 1989). A list of some mortality events in cockles and promulgated causes are listed in Table 1.

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Table 1. Published 'mass' mortality events reported for *Cerastoderma edule*. No mass mortality events have been noted for *Cerastoderma glaucum*. ND, no data.

Geographical locality	Age affected	Promulgated cause	Date	Reference
Burry Inlet, UK	ND	Unknown	Summer 1959	Hancock & Urquhart (1965)
Burry Inlet, UK	ND	Predation	Winter 1960–62	Hancock & Urquhart (1965)
Burry Inlet, UK	ND	*Bucephalus minimus sensu lato*?	Winter 1962–63 Summer 1965	Bowers (1969)
Burry Inlet, UK	ND	*Gymnophallus minutus*/stress	Winter 1974/1975	James *et al.*, (1977)
Burry Inlet, The Wash, Thames, Whitstable, Morecambe Bay, UK	ND	Harsh winter conditions—exposure	Winter 1962–63	Hancock & Urquhart (1964)
Lancashire and Cheshire, UK	ND	Unknown—reproductive stress?	Summer 1933	Orton (1933)
Exe Estuary, UK	>2 years old	*Gymnophallus minutus*	Summer	Goater (1993)
The Wash, UK	ND	Unknown	Since 1987	Atkinson *et al.* (2003)
Wadden Sea, The Netherlands	ND	Exposure	Winter 1970/1971 Winter 1979/1980 Winter 1985/1986 Winter 1986/1987 Winter 1987/1988 Winter 1995/1996[1]	Beukema *et al.* (2010); Reise (2003); Strasser *et al.* (2001b)
Wadden Sea, The Netherlands	ND	'Delayed mortality' from winter	Summer 1996	Strasser *et al.* (2001a)
Wadden Sea, The Netherlands	ND	*Gymnophallus gibberosus*	Winter 1992/1993	Thieltges *et al.* (2008)
Wadden Sea, The Netherlands	ND	*Gymnophallus choledochus*	Summer 2004	Thieltges (2006)
Wadden Sea, The Netherlands	ND	Predation by oystercatchers and overfishing, poor recruitment	Winter 1978/1979; Winter 1984/1985; Winter 1985/1986; Winter 1986/1987; Winter 1990/1991	Beukema (1993); Jensen (1992)
Bay of Somme, France	ND	Eutrophication	Summer 1981–1985 Summer 1989 Summer 1990	Desprez *et al.* (1992); Rybarczyk *et al.* (1996)
Bay of Morlaix, France	Juveniles	Predation by crabs	Summer 1993	Masski & Guillou (1999)
Bay of Morlaix, France	1 month/ 1 year	Low glycogen reserves and predation	Winter 1987–1991	Guillou & Tartu (1994)
Portugal	ND	Amoeba	Summer?	Azevedo (1997)
Portugal	ND	*Mycoplasma*-like organisms	Summer 1991 and 1992	Azevedo (1993)
Portugal	ND	*Nematopsis* sp.	ND	Azevedo & Cachola (1992)
Galicia, Spain	ND	Granulocytomas (*Minchinia*) and disseminated neoplasia	Summer 1997	Carballal *et al.* (2003); Villalba *et al*, (2001)
Galicia, Spain	ND	Disseminated neoplasias	Spring 1999	Ordás & Figueras (2005)
Sweden	ND	*Monorchis parvus*	Summer 1991	Jonsson & André (1992)
Sweden	3 months/ 1 year	Predation by crabs	-	Möller & Rosenberg (1983)

[1], includes mortality of *C. glaucum* in winter 1995/1996.

Ducrotoy *et al.* (1989) developed a simple model of population parameters. These included populations undergoing 'crisis' situations characterized by a few age-classes which undertake successive spawning-periods or uninterrupted spawnings leading to numerous cohorts. This is considered a strategy for restoration by the cockle. A single and strong recruitment leading to a high density of the first cohort then occurs in the 'recovery' phase with the possibility of synchronization of spawning between breeding stocks. The most ideal population is one defined as 'upholding' by Ducrotoy *et al.* (1989) in which there are several age-classes and a higher density of older age-classes with spawning following the expected pattern. Any subsequent collapse in abundance may be due to loss of older animals and/or unsuccessful recruitment. Any increase in population growth rate at this stage should be considered as a sign of instability which may lead to a population crash.

GENETICS

Controversy has existed regarding the genetic relationship between *Cerastoderma glaucum* and *C. edule* with a number of molecular and morphological techniques (including shell and sperm morphology) being used to discriminate the species from each other (Rygg, 1970; Urk, 1973; Brock, 1987; Chao, 2000). These techniques and others have subsequently been applied to discriminate larvae and adults as well as to demonstrate the phylogeny and phylogeography of cockle populations. Isozyme and allozyme electrophoresis studies with *C. edule* and *C. glaucum* are readily able to discriminate the two species (Jelnes *et al.*, 1971; Brock, 1987; Machado & Costa, 1994) and discriminate subpopulations of both species throughout their range (Hummel *et al.*, 1994; Mariani *et al.*, 2002; Nikula & Väinölä, 2003). Electrophoretic methods provide limited evidence for genetically isolated populations of *C. edule*. However, Beaumont & Pether (1996) suggested that cockles from the Burry Inlet (Wales) appeared to be distinct from seven other cockle populations around the UK sampled for nine polymorphic allozyme loci. It should be noted that allozymes may be subject to selection, and therefore differences in allele frequencies between populations could be selectively induced, rather than representing true genetic differences. Lagoon cockles collected from the infralittoral zone of the Romanian Black Sea were mainly shown to be similar, with over 80% of the animals sharing similar haplotypes (David & Tigan, 2011).

Studies using microsatellite data have further shown that the allele frequency of cockles indicated low but significant genetic differentiation of populations of cockles around the estuaries of UK coasts but that localized samples showed no significant difference (e.g. Burry Inlet). This suggests that the Burry Inlet at the time of study was thought of as a single population even though the presence of a pelagic larval phase would suggest the potential for extensive dispersal. Molecular methods have shown that at least two dominant haplotypes of *C. edule* occur—a homogeneous south-western population from Africa to the British Isles and a second haplotype of a heterogeneous northern group predominately in the Arctic (Krakau *et al.*, 2012). A more complex population structure of *C. glaucum*, formed as a result of its fragmented distribution has been shown through mtDNA data (Tarnowska *et al.*, 2010). As a result of that study, Tarnowska *et al.* (2010) suggested that the taxonomy of the genus required revision.

Chromosome patterns have some utility for discriminating subpopulations of *C. glaucum*. Both edible and lagoon cockles have a diploid chromosome complement of $2n = 38$ (Wolowicz & Thiriot-Quievreux, 1997; Leitão *et al.*, 2008). The karyotype of lagoon cockles from the southern Baltic Sea includes 11 metacentric, 2 submetacentric and 6 subtelocentric chromosomes (Wolowicz & Thiriot-Quievreux, 1997) whilst those from Gdansk Bay have 3 metacentric, 10 submetacentric and 6 subtelocentric chromosome pairs (Thiriot-Quievreux & Wolowicz, 1996). In contrast, those from Thau Lagoon in the Mediterranean have a karyotype of 4 metacentric, 9 submetacentric and 6 subtelocentric pairs (Thiriot-Quievreux & Wolowicz, 1996). In general *C. edule* has a karyotype of 12 submetacentric, 3 telocentric and 4 subtelocentric chromosomal pairs or 7 submetacentric, 5 telocentric and 7 subtelocentric depending on geographical origin (Insua & Thiriot, 1992). However, in the presence of environmental pollutants the number of chromosomes can dramatically increase as a result of chromosomal fission and may thus have some utility as a biomarker for contaminant exposure (Insua & Thiriot, 1992; Leitão *et al.*, 2008).

Cockle species have been discriminated from each other and from other bivalve species through the use of molecular methods such as random amplified polymorphic DNA (RAPD-DNA) (André *et al.*, 1999), polymerase chain reaction (PCR) and sequencing of 18S rRNA, 5S rDNA/RNA, ITS1 and ITS2 (Insua *et al.*, 1999; Hare *et al.*, 2000; Freire *et al.*, 2005, 2009, 2011; Larsen *et al.*, 2005, 2007; Espineira *et al.*, 2009), PCR-restriction fragment length polymorphism (PCR-RFLP) (Freire *et al.*, 2005) and single-strand conformation polymorphism-PCR (SSCP-PCR) (Nikula & Väinölä, 2003). All methods are equally valid in discriminating species.

REPRODUCTION AND DEVELOPMENT

As with most bivalves, cockles are dioecious with no external morphological differences between the sexes. In general, there is a 1:1 sex-ratio in any given population (Boyden, 1971; Bowmer *et al.*, 1994). Discrepancies in these ratios may provide evidence of a sex-specific mortality. Reproductive cycles for *Cerastoderma edule* and *C. glaucum* are similar with rapid gametogenesis occurring in spring. Subsequent maturation of *C. edule* occurs at a quicker rate compared with *C. glaucum*, which may reduce the risk of cross-fertilization in sympatric populations of these species (Boyden, 1971). However, Brock (1982) considered that synchronous spawning occurred in sympatric species although hybrids were not produced as a result. Some limited evidence of hybridization has however been provided (Kingston, 1973).

Cerastoderma species undergo gametogenesis in February/March followed by rapid gonad development in April and May and spawn around May to July/August with gonads accounting for up to 20% of the animal's body mass at the height of sexual maturity (Lebour, 1938; Boyden, 1971; Newell & Bayne, 1980; Brock, 1982; Guillou *et al.*, 1990; Cardoso *et al.*, 2009). Some populations of *C. glaucum* undergo two to three synchronized spawning events (spring and autumn) (Zaouali, 1980; Derbali *et al.*, 2009a); *C. edule* either undergoes a single spawning event in a short space of time (Kingston, 1974a) or can undertake 'polycyclic' spawning without a resting period (Yankson, 1986b). Gonadal resting takes place usually between October and March. Egg production and egg size is larger after a harsh winter compared with mild winter temperatures (Honkoop *et al.*, 1995) and although recruitment is generally earlier after a mild winter (Strasser *et al.*, 2001a), survival of progeny may be lower (Beukema *et al.*, 1993). Exposure to various pollutants such as pulverized fuel ash, polyaromatic hydrocarbons, polychlorinated biphenyls or oestrogenic compounds can delay the onset of oocyte maturation and reduce fecundity (Bowmer *et al.*, 1994; Timmermans *et al.*, 1996; Matozzo & Marin, 2007). In addition, certain parasites such as digeneans have been shown to castrate both males and female cockles reducing reproductive output of a population (Boyden, 1970; Derbali *et al.*, 2009a).

Various schemes to categorize the development stages of the gonad have been proposed including by Boyden (1971) for *Cerastoderma* spp. who listed grades I to IV representing resting (or spent), developing, ripe and very ripe respectively. A similar, but somewhat extended scheme for female *C. edule* was suggested by Seed & Brown (1977) with 0 being rested or spent, 1 and 2 developing and spawning, 3 being ripe. For male cockles the scheme proposed by Boyden (1971) was grade 0 (indeterminate), grade II (developing), grade III (ripe) and IV (very ripe/spawning); the scheme for male cockles proposed by Seed & Brown (1977) mirrored that proposed for female cockles. The scheme of Kingston (1974a) consisted of stage 1 (initiation of gametogenesis), stage 2 (development), stage 3 (ripe), stage 4 (recently spawned) and stage 5 (post-spawning recovery).

Minimum size at first maturity in *C. glaucum* is normally around 12 mm shell length (SL) for males and 14 mm SL for females (Derbali *et al.*, 2009b); similar sizes have been reported for *C. edule* (Hancock & Franklin, 1972; Seed & Brown, 1977). Maturation of 7 weeks old *C. glaucum*

(4 mm SL) laboratory reared spat has been reported and although no fertilization experiments were conducted, gamete morphology was comparable to those of adults from natural populations (Yankson, 1986a). Edible cockles produce many, small pelagic eggs whilst lagoon cockles produce a smaller number of larger benthic eggs (Reise, 2003). Eggs become non-viable if not fertilized within 4–8 hours post-release from the females (André & Lindegarth, 1995). Following fertilization, eggs are pelagic with larval development in the pelagic phase taking around 31/2 to 5 weeks; the veliger stage accounts for around 2 to 3 weeks of this (Lebour, 1938; Creek, 1960).

Although many bivalves typically undergo a lifecycle that includes a planktonic dispersal phase followed by a sessile juvenile stage (a plantigrade) with metamorphosis into an adult, cockles have been shown to undergo a secondary, planktonic postlarval stage (Baker & Mann, 1997). Secondary dispersal of edible cockle larvae is restricted to the summer months in northern Europe and is correlated with a semilunar rhythm of 15 days (Armonies, 1992). In contrast, planktonic *C. edule* larvae occur throughout most of the year in southern Portugal (Chicharo & Chicharo, 2000). This planktonic postlarval dispersal is an active process occurring in cockles up to 6 mm in length (de Montaudouin, 1997; de Montaudouin *et al.*, 2003). Survival and subsequent recruitment of cockles into the adult population can be influenced by a number of factors including predation, climate, larviphagy and sediment dynamics (Jensen & Jensen, 1985; André & Rosenberg, 1991; Young *et al.*, 1998; Bouma *et al.*, 2001; Flach, 2003; Beukema & Dekker, 2005).

FOOD, FEEDING, ENERGY AND GROWTH

Cockles are generalist, opportunistic filter feeders (Rueda & Smaal, 2002), with food captured by the gills, enclosed in a mucus secretion derived from the cockle and transported to the mouth (Foster-Smith, 1975). This opportunism is beneficial as it limits inter-specific competition for food (Lefebvre *et al.*, 2009). Cockles are able to preselect particles for ingestion via the gills and show a strong preference for organic material (Iglesias, 1992). Production of pseudofaeces as a result of this process limits the amount of energy expended in digesting poor quality food (Urrutia *et al.*, 2001). Cockles are able to adjust the different digestive enzymes depending on food quality and quantity, particularly with respect to amylases and cellulases (Ibarrola *et al.*, 1996, 1998a). In addition, seasonal changes in these digestive enzymes occur, with increased amounts being available during spring and summer in response to increased food availability (Ibarrola *et al.*, 1998b). The maximum peak of activity appears to be linked to maximum activity in growth therefore maximizing energy balance from improved nutritional conditions (Ibarrola *et al.*, 1998b). As a predominately suspension feeding organism, it is not surprising to find that algal species found in the stomach of cockles correlates well with the species composition in the water column (Kamermans, 1994). During the tidal cycle when the tidal flats are drained, minimal levels of algae are found in the stomachs of cockles, supporting the view that food intake is extremely limited during this period (Kamermans, 1994), which in turn affects growth (Jensen, 1992). Age related differences in food choices are noted with juveniles and spat reliant on the microphytobenthos (algae) whilst adults feed on a combination of both suspended particulate organic matter (Kang *et al.*, 1999; Karlsson *et al.*, 2003; Rossi *et al.*, 2004) derived from marine plants such as the sea rush *Juncus maritimus* Lamm., small cordgrass *Spartina maritima* (Curtis) and the green macroalgae *Ulva* (=*Enteromorpha*) sp. (Sarà, 2007; Arambalza *et al.*, 2009, 2010) and feeding on phytoplankton (Navarro *et al.*, 2009). Data on feeding habits of planktonic larval stages of cockles are lacking although Bos *et al.* (2006) implies that pelagic larval stages of *C. edule*, like other marine bivalves, feed predominately on small phytoplankton, including dinoflagellates, diatoms, ciliates and bacteria. This lack of data requires further investigation. Using an *in vitro* preparation of the gills, Bamford & McCrea (1975) were able to show that *Cerastoderma edule* absorbed L-alanine and L-lysine via a carrier mediated process and via a saturable system respectively. Absorption of these environmentally derived amino acids is considered to be an important source of nutritional supplements in other bivalves (Wright, 1982).

Bivalves exposed to chronic disturbance by fisheries or other forms of disturbance, such as disease or contaminants, incur greater energetic costs related to physical damage and stress which affects body condition and gonad development (Kaiser *et al.*, 2007), in addition to more subtle short-term effects on their immunocompetence. It is known that cockle growth is strongly influenced by seasonality. A seasonal change in soft body weight occurs, which is dependent on food supplies, metabolic rate and maintenance requirements (Navarro *et al.*, 1989). Seasonal changes in dry weight are as expected and reflect the reproductive cycle with weight loss during spawning and over winter. Weight loss is proportionally larger in older cockles compared with younger individuals (Beukema & Dekker, 2006).

Honkoop & Beukema (1997) suggested that cockles lose body mass in autumn and winter due to low food supply and high temperatures causing high energy demands. Zwarts (1991) found a relationship between temperature and changes in body mass index, with lower temperatures causing lower body mass loss at the end of winter and greater reproductive output than at higher temperatures where more energy is utilized for maintenance and growth. Carbohydrate and glycogen tend to show an interannual variation with a maximum in December followed by a decline as the gonad developed in young cockles (Navarro *et al.*, 1989). Navarro *et al.* (1989) demonstrated that after spawning there is a period of recovery of the carbohydrate and glycogen levels in the cockle until July followed by a decline through to February of the following year. Although the lipid content of the tissues did not alter over the study period of about 19 months, the protein content was negatively correlated to the carbohydrate levels with maximum carbohydrate occurring at the same time as protein minima. Glycogen accumulation occurred in early summer in the Navarro *et al.* (1989) study whereas Boyden (1971) demonstrated that it occurred in the summer and early autumn. Differences in glycogen uptake could be due to environmental factors such as the availability of food and different experimental sites as well as the experimental method. Bivalve digestion appears to be biphasic and involves extracellular digestion of ingested food particles mediated by the action of the crystalline style and subsequent intracellular digestion within the digestive gland (Ibarrola *et al.*, 1998b). These authors showed that cockles are able to increase their cellulose activities in the digestive gland, ten times more than in the style, when there is more food around by increasing the size of the digestive gland including its specific cellulose activity.

PREDATORS

Cockles are an important component of the ecosystem and are a major food source for a number of species, in particular for birds that actively forage for cockles during low tide. Cockles, in particular *Cerastoderma edule* are commercially fished by man. Invertebrates such as the brown shrimp *Crangon crangon* (Linnaeus, 1758) predate on small postlarvae (newly settled spat) (Beukema & Dekker, 2005) whilst the common shore crab *Carcinus maenas* (Linnaeus, 1758) feeds on a wider size-range of cockles, consuming approximately 40 *C. edule* per individual per day (Sanchez-Salazar *et al.*, 1987). In a field caging experiment in Sweden, Flach (2003) showed that allowing crabs access to cockles in selected plots led to reduction in cockle recruitment success by nearly 90% and suggested that a combination of high predation rates and the presence of high densities of adult macrofauna led to recruitment failures of *C. edule*. Similar results were obtained for cockles smaller than 11 mm in length in Brittany (Masski & Guillou, 1999). However, whilst acknowledging that predation by juvenile crabs on young cockles was an important factor in determining survival in the Wadden Sea, Jensen & Jensen (1985) only considered that about 6% of the total cockle production was compromised by predation by crabs. Size-selective feeding by *C. maenas* on cockles occurs with large crabs (carapace length 55–70 mm) selecting cockles 10–20 mm long compared with medium sized crabs (carapace length 40–55 mm) having a preference for cockles with a shell length of 5–10 mm (Mascaró & Seed, 2000a, b). Differences in predation rates of crabs on *Macoma balthica* (Linnaeus, 1758) and *C. edule* have been noted (Richards *et al.*, 1999) and this may be due to the response of *M. balthica* to crab-derived chemical cues. When cockles and *M. balthica* were exposed to chemical cues emitted from shore crabs, *M. balthica* responded by doubling their burial depth; cockles failed to respond to these cues making them 15 times more likely to be predated on compared with *M. balthica* (Griffiths & Richardson, 2006). The identity of the chemical cue remains unknown.

Gastropods such as *Nucella lapillus* (Linnaeus, 1758), *Hexaplex* (*Trunculariopsis*) *trunculus* (Linnaeus, 1758), *Euspira* (=*Polinices*) *pulchella* (Risso, 1826) and *Buccinum undatum* Linnaeus, 1758 predate on *C. edule* by either drilling through or by prising open the shell but they are not considered to dramatically influence cockle population dynamics (Morgan, 1972; Kingsley-Smith *et al.*, 2003; Morton *et al.*, 2007; Scolding *et al.*, 2007). The polychaete *Halla parthenopeia* (Delle Chiaje, 1828), whilst having a preference for *C. glaucum* under experimental conditions, only consume around 1 cockle each per day (Osman *et al.*, 2010). Larviphagy, the feeding on bivalve larvae by adult bivalve filter feeders, has been reported for a number of species, including *Crassostrea gigas* (Thunberg, 1793) and *Mytilus edulis* Linnaeus, 1758 (Troost *et al.*, 2008). Adult *C. edule* can reduce settlement of *C. edule* larvae by up to 40% through this route (André & Rosenberg, 1991) although they can ingest up to 75% of larvae drifting over the sediment populated by adult cockles (André *et al.*, 1993).

Predation by *Pomatoschistus microps* (Krøyer, 1838) on post-settlement *C. glaucum* can account for 50–70% of the mortalities encountered for this life stage (McArthur, 1998) whilst *C. glaucum* account for up to 60% of the diet of *Rutilus frisii* (Nordmann, 1840) (Afraeibandpei *et al.*, 2009) and they can be a component of the diet of *Rutilus rutilus* (Linnaeus, 1758) in the Baltic Sea (Rask, 1989). Larger sized *C. edule* (5–10 mm in size) can be the dominant food item for flounder and plaice, particularly in late summer and early autumn and for older fish (De Vlas, 1979; Pihl, 1982). As well as feeding on whole cockles, plaice and flounder have a high predation rate on the foot tips and siphons of *C. edule* (De Vlas, 1979). The impact of this sublethal predation on cockle survival and increased susceptibility to additional predation is unknown. However, New Zealand cockles (*Austrovenus stutchburyi* (Wood, 1828)) with cropped feet are unable to bury before the foot has regenerated and are thus more susceptible to thermal and desiccation stress as well as being subjected to a substantially higher predation risk (Mouritsen & Poulin, 2003).

Oystercatchers (*Haematopus ostralegus* Linnaeus, 1758) and knot (*Calidris canutus* (Linnaeus, 1758)) are major avian predators of cockles with sanderling (*Calidris alba* Pallas, 1764), grey plover (*Pluvialis squatarola* (Linnaeus, 1758)), redshank (*Tringa tetanus* (Linnaeus, 1758)), eider (*Somateria mollissima* (Linnaeus, 1758)), common gull (*Larus canus* Linnaeus, 1758) and long tailed duck (*Clangula hyemalis* Leach, 1819) predating on this host to a lesser extent (Drinan, 1957; Bryant, 1979; Sutherland, 1982; Dekinga & Piersma, 1993; Cadee, 1994; Triplet, 1994; Stempniewicz, 1995; Perez-Hurtado *et al.*, 1997; Beukema & Dekker, 2006). Individual birds are estimated to take up to 300 cockles per day. Oystercatchers preferentially feed on second winter and larger cockles (>15 mm) when numbers of cockles are high but switch to feeding on smaller cockles (<15 mm) when numbers of cockles are depleted (O'Connor & Brown, 1977; Johnstone & Norris, 2000). Larger, older cockles tend to have the highest helminth intensity but are also energetically the most profitable prey (Norris, 1999). In addition, parasites such as digeneans may alter burrowing behaviour leading to increased predation. Thus feeding on larger cockles can increase the risk of exposure of birds to parasites, particularly as oystercatchers do not selectively feed on non-parasitized cockles (Norris, 1999). Ultimately, several thousand digeneans can occur in individual oystercatchers with a concomitant impact on bird survival (Borgsteede *et al.*, 1988).

IMMUNOLOGY

The ability of animals or plants to defend themselves against disease can be linked directly to the 'quality of the surrounding environment' (Oliver & Fisher, 1999). Animals and plants protect themselves from infection mainly via the detection of pathogens and the capacity of the immune system to mount a response. In invertebrates, haemocytes are capable of recognition, migration and phagocytosis of foreign microorganisms and possible internal or external microbicidal superoxide generation (Millar & Ratcliffe, 1994). The haemolymph contains lectins and opsonins which coat the foreign organisms and enable faster recognition by the haemocytes (Millar & Ratcliffe, 1994). The haemocytes of *Cerastoderma edule* and *C. glaucum* have been shown to be similar to the haemocytes of other bivalves containing both agranular (hyaline) cells and both eosinophilic and basophilic granular haemocytes. However there is a third type of cell that has been described as Type III eosinophil cell (Russell-Pinto *et al.*, 1994; Wootton *et al.*, 2003b; Matozzo *et al.*, 2007) which contains a large vacuole potentially used for nutrient or enzyme storage. The granular cells of *C. edule* stain positively for the enzymes non-specific esterase, acid phosphotase (Russell-Pinto *et al.*, 1994), arylsulphatase and peroxidase (Wootton *et al.*, 2003b). Wootton *et al.* (2003b) also demonstrated that lectin-binding in *C. edule* was similar to other bivalves such as *Mytilus edulis*. Interestingly in *C. glaucum*, unlike other bivalves, it appears that hyalinocytes are also able to phagocytose (Matozzo *et al.*, 2007).

Functional differences in immunocompetence were also detected between *C. edule*, *C. glaucum* and *M. edulis* haemocytes where the cockle haemocytes were less phagocytically active, had lower superoxide generation and fewer lysosomal enzymes (Wootton *et al.*, 2003b; Matozzo *et al.*, 2007). These findings potentially suggest that cockles are more sensitive to environmental stress compared to mussels; however, the results may be a matter of the more restricted lifecycle of the more infaunal burrowing cockle. Stress responses and reduced immunocompetence have been shown in a number of molluscs after exposure to environmental stresses including temperature, inorganic nutrients and their interaction (Malham *et al.*, unpublished data), salinity (Gagnaire *et al.*, 2006) bacteria and physical stress (Lacoste *et al.*, 2001; Malham *et al.*, 2003).

EXTRINSIC ENVIRONMENTAL DRIVERS

Marine bivalve molluscs, including cockles, are well known to be sensitive to a wide variety of chemical contaminants found in coastal environments. Depending on the physico-chemical properties of the contaminants of interest, chemicals may accumulate in marine sediments (in general these are more hydrophobic organic chemicals with a log P of >3) or may tend to remain in the water column. Hence it is important to take into account both the water and sediment exposure aspects for chemicals of concern for the environmental quality and the health of shellfish populations, as well as bearing in mind the life cycle of cockles or other organisms of relevance. In general, early developmental stages are often the most vulnerable to chemical toxicants and often represent a critical period in the lifecycle of marine invertebrate. For example, it is known that copper, mercury and zinc are toxic to oysters and other marine invertebrate larvae at levels 14 to 1000 times lower than to adults (Connors, 1972). With this rationale, mussel and oyster embryo development toxicity tests are widely used in Europe as highly sensitive monitoring tools for the presence of toxic chemical contaminants (for example, see Thain, 1991; His *et al.*, 1999; Beiras & Bellas, 2008).

There is a lack of data on the overall health, and in particular negative effects, of individuals and populations of cockles as a result of exposure to radioactivity, shellfish poisoning (including diuretic, paralytic, amnesic and azasparacid shellfish poisoning), nutrient enrichment or sewage in spite of their apparent importance and known impacts in other bivalve species (Svensson *et al.*, 2000; Vale & De, 2002; Furey *et al.*, 2003; Miles *et al.*, 2004; Vale, 2004; Stobo *et al.*, 2005; Scotter & Roberts, 2007; Gunsen *et al.*, 2008; Vale *et al.*, 2008; Vale, 2010). Numerous papers have, however, dealt with the uptake, sequestration, bioaccumulation, and tissue localization of these compounds (Jaime *et al.*, 2007). For example, cockles will readily take up radioactive particles from sediment and water, although there is evidence of preferential uptake for different elements and indeed that uptake from contaminated sediment is almost negligible compared with uptake from water (Miramand & Germain, 1985; Germain *et al.*, 1987). Cockles preferentially accumulate plutonium (^{239}Pu) at a rate 8 times higher compared to americium (^{241}Am) and reach equilibrium more quickly (Miramand & Germain, 1985). In addition, differences in target organs were noted with plutonium being fixed in the flesh, pallial organ and shells whilst americium is fixed mainly in the viscera and digestive tract. Similar results have been obtained for exposure of cockles to curium (^{244}Cm), lead (^{210}Pb) and polonium (^{210}Po) (Miramand *et al.*, 1987; Jia *et al.*, 2003).

In contrast, the impact of hydrocarbons, including polyaromatic hydrocarbons (PAHs) has been extensively studied in cockles (Porte *et al.*, 2000; Carro *et al.*, 2006; Fernandes *et al.*, 2009). Typically, DNA damage, measured by the comet assay has been shown to occur (Fernández-Tajes *et al.*, 2011; Pereira *et al.*, 2011), as well as alterations to immune function (Wootton *et al.*, 2003a) and gonadal development (Timmermans *et al.*, 1996). Barite, used to lubricate and cool drill bits as well as control well pressures in the offshore oil industry, can damage gill architecture of *C. edule* including destruction of the cilia and ultimately complete loss of gill function and death (Barlow & Kingston, 2001). Pulverized fuel ash (PFA) or fly-ash, a by-product of coal burning for production of electricity typically contains high levels of metals and has commonly been dumped at sea (Bowmer *et al.*, 1994). Cockles exposed to PFA show high mortality rates and reductions in and delays to reproductive output; histological changes in the digestive gland have also been recorded (Jenner & Bowmer, 1990; Bowmer *et al.*, 1994). Metal contamination of sediment has been shown to reduce burrowing behaviour (Amiard & Amiard-Triquet, 1986) whilst parasitism can lead to increased vulnerability to metal contamination (Baudrimont *et al.*, 2003, 2006; Baudrimont & de Montaudouin, 2007; Desclaux-Marchand *et al.*, 2007; Paul-Pont *et al.*, 2010). High levels of metals may be accumulated at different rates in different tissues of cockles, and indeed sequestered at a higher rate compared with environmental levels, thus any surveys conducted to assess metal contamination must consider this (Cheggour *et al.*, 2001; Baudrimont *et al.*, 2005).

Cockles from highly polluted areas can be exposed to a number of contaminants, including endocrine disruptors. Matozzo & Marin (2007) examined cockles at the very early stage of gametogenesis (January) and in the pre-spawning period (June) from Venice lagoon. Animals from the more contaminated sites had higher vitellogenin-like protein levels compared with other sites. The authors consider that endocrine disrupters have the capacity to lead to fertility reductions, alterations in sex-ratios and reductions in reproductive rates. In a further refinement, Matozzo *et al.* (2008) reported on the effects of the xenoestrogen 4-nonylphenol

(NP) on functional responses of haemocytes from the cockle *Cerastoderma glaucum*. Adult cockles were exposed to sublethal NP concentrations for seven days, after which aspects of the haematology of the animals were assessed. Total haemocyte count, lysozyme-like activity and acid phosphatase activity were generally significantly increased in animals exposed to NP. Subsequently, Marin *et al.* (2008) conducted experimental work to define the lethal and sublethal effects of 4-nonylphenol in the cockle *Cerastoderma glaucum*. In a 96-h lethality test, the LC_{50} value was 0.3 mg NP/l with no mortalities being observed at 0.1 mg NP/l. Furthermore, the authors were able to show that NP induces vitellogenin synthesis in *C. glaucum* and that males were more responsive to NP compared with females. Whilst the study was able to demonstrate similar effects between sexually undifferentiated (resting phase) and differentiated (pre-spawning phase) cockles, to date no experimental studies have been found on the effects of chemicals on the early life stages of cockles. Importantly, the combination of chemical contaminants and pathogens could have a serious impact on the health of mollusc populations. For a recent review of the importance of understanding the role of environmental stressors such as chemical contaminants on disease resistance in molluscs see Morley (2010).

Salinity has an impact on the distribution and survival of cockles. *Cerastoderma glaucum* tends to occur in lagoons and salt marshes and thus would naturally be exposed to higher salinities compared with *C. edule* which occur on more open coasts and in estuaries where salinities may show a greater diurnal variation. Kater *et al.* (2006) suggest that salinity has less of an influence on cockle distribution compared with flow velocity and emersion time. However, they do acknowledge that low salinity will ultimately limit distributions. *Cerastoderma edule* has a preference for salinities of between 12.5 and 38.5 (ppt) (Russell & Petersen, 1973), whilst *C. glaucum* can tolerate salinities of between 15 and 35 (Boyden & Russell, 1972). Optimal salinity for both species is between 30 and 35 (Kingston, 1974b). If exposed to sudden reductions in salinity i.e. influx of freshwater, *C. glaucum* will undergo complete closure of the valves whilst *C. edule* will partially close its valves and undergoes periodic gaping movements (Nossier, 1986). Nossier (1986) demonstrated that both species of cockles respond to rhythmic changes to the tidal flows and suggested that *C. edule* is more able to respond on a daily basis to fluctuating environmental conditions whilst *C. glaucum* were likely to respond more positively to seasonal changes in environmental conditions. However, any dramatic alterations in salinity can only really be tolerated for short periods before mortalities are induced. Salinity tolerances of cockle larvae are lower compared with adults as they are only able to tolerate salinities as low as 20–25, and can frequently be deformed if reared at salinities of 20. Furthermore, whilst they are able to grow at salinities of 40, at salinities of 45 they are unable to undergo metamorphosis (Kingston, 1974b).

Tolerances to thermal stress can vary depending on the season and physiological state of animals. In addition, age can influence tolerance with young *C. glaucum* being more resistant to short exposures to high temperatures compared to adults (Ansell *et al.*, 1981). Compton *et al.* (2007) showed that *C. edule* were able to tolerate temperatures of between +4°C and +38°C. Geographical and seasonal differences in upper thermal tolerance which may reflect historical exposures to temperature extremes are noted with upper thermal tolerances of up to 45°C noted for *C. glaucum* from France and Ireland collected in summer compared with an upper limit of 40°C for *C. glaucum* collected in winter from Ireland (Wilson & Elkaim, 1997). Extreme low winter temperatures have been implicated in population mortalities of cockles, particularly *C. edule* throughout their range (see Table 1). Temperature can also influence egg production, with higher temperatures leading to smaller sized and fewer numbers of eggs being produced in *C. edule* (Honkoop & van der Meer, 1998). However, fertilization does not occur below 5°C and viable offspring are not produced at temperatures above 25°C (Kingston, 1974b). In contrast, further development of larvae can occur at higher temperatures of 25–30°C for *C. edule* and 30–35°C for *C. glaucum* whilst growth is retarded at 10°C or lower (Kingston, 1974b).

Cockles are able to consume oxygen from the air if removed from the water, albeit at a lower rate compared with oxygen consumption when immersed (Widdows *et al.*, 1979). Gaping of bivalves during aerial exposure allows for oxygen diffusion into the mantle water and for *C. edule* aerial uptake rate of oxygen is between 28 and 78% of the aquatic rate; for *C. glaucum* aerial uptake rate is much lower at 8% of the aquatic rate (Widdows *et al.*, 1979). Anaerobic metabolism does occur in cockles, but at a lower rate compared with other bivalves such as *Macoma balthica* and *Mytilus edulis* which tend to show less of a gape response on exposure to air (Ahmad & Chaplin, 1984). Anaerobic bacteria and digenean parasites can greatly reduce survival time of *C. edule* under anoxic or air-exposed conditions (Wegeberg & Jensen, 1999; Javanshir, 2001; Barbarro & de Zwaan, 2008). It is possible that some perceived mortalities of *C. edule*, reported as gaping, may reflect the normal aerial breathing behaviour of the species. Thus caution should be exercised in the interpretation of reports of mortalities described in this fashion in the absence of empirical evidence to support such a view.

CONCLUSIONS AND FUTURE DIRECTIONS

This review has covered the major aspects of the biology and health of cockles and considered those factors that influence their individual and population health. It became clear throughout that a number of issues and priority knowledge gaps need to be addressed. In particular, there is a lack of information on basic biology of cockle larvae including dispersal mechanisms and the influence of environment on cockle lifecycles. This includes the alternation between benthic and pelagic phases. The different approaches taken by different researchers to measure life spans and age of cockles have created issues when comparing the literature. Research should be directed towards clarifying the growth rates of cockles, including measuring daily growth as well as annual growth. Understanding the diet choices and the types of predators appears to be well mapped out although it is unclear about the overall impact of predators on population health and this should be assessed as a matter of priority. There is a lack of data on the food habits of pelagic cockle stages. In addition, the effect of food quality on host fitness and disease resistance needs to be considered.

Future climate change scenarios broadly predict that temperatures will generally increase and that precipitation will decrease in the summer months and increase during winter months (Johnson *et al.*, 2009). In coastal zones, particularly in vulnerable estuarine areas, this is likely to manifest as a decrease in salinity during winter months due to increased freshwater inundation and higher temperatures during summer months. Furthermore, increases in storm and flooding events may affect the overall stability of these ecosystems with a fundamental shift in the types of organisms present. It is not clear how estuaries will be affected by perceived changes in ocean acidification. Bivalve recruitment, in particular of cockles, is likely to be detrimentally impacted by increased winter temperatures (Beukema, 1992; Beukema & Dekker, 2005; Cardoso *et al.*, 2009) although the predicted decrease in the frequency and severity of cold winters under future climate change scenarios may lead to fewer mortalities of adult populations (e.g. Hancock & Urquhart, 1964; Beukema *et al.*, 2010). Flooding events in estuaries that are already environmentally stressed are likely to be more detrimental to cockles than other species in these systems (Cardoso *et al.*, 2008) whilst genetically homogeneous cockle populations may be less able to cope with environmental changes in general.

An integrated approach should be used in all future studies of cockles (Jung *et al.*, 2006; de Montaudouin *et al.*, 2010). This should include ensuring that contemporaneous samples are examined (or at least collected) for a range of studies at the same time. The lack of phenotypic anchoring as a result of failure to collect such samples can lead to erroneous interpretations of the results obtained. It is clear from studies of mortality events that it is difficult to unequivocally assign a cause to the host deaths due mainly to the lack of all relevant biological and ecological data being collected. As a guide, during routine cockle studies the following data should be obtained: length, age and growth; molecular samples to confirm species identity as well as population genetic stock and the health and reproductive status should be assessed. Other measures such as density, estimates of mortality rates, associated fauna, sediment type, salinity, temperature and water quality should also be collected.

There is a need to better understand exposure risks associated with the particular life stage of the cockle comparing benthic and pelagic habitats and ensuring that ecological quality standards that have been derived for other species are appropriate for cockles. In addition, it is important to collate the available chemical monitoring data for metals and organic contaminants monitored by responsible bodies in areas of cockle fisheries and to identify key data gaps for chemical classes of interest (including emerging chemical contaminants such as endocrine disrupters). Finally, it will be important to develop methods to assess immune function in adult and early life stages of cockles for use in field and laboratory studies to assess disease resistance opposite environmental stressors (e.g. chemicals, hypoxia, temperature, etc).

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