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Ecosystem services provided by a non-cultured shellfish species: The common cockle *Cerastoderma edule*

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ABSTRACT

Coastal habitats provide many important ecosystem services. The substantial role of shellfish in delivering ecosystem services is increasingly recognised, usually with a focus on cultured species, but wild-harvested bivalve species have largely been ignored. This study aimed to collate evidence and data to demonstrate the substantial role played by Europe's main wild-harvested bivalve species, the common cockle *Cerastoderma edule*, and to assess the ecosystem services that cockles provide. Data and information are synthesised from five countries along the Atlantic European coast with a long history of cockle fisheries. The cockle helps to modify habitat and support biodiversity, and plays a key role in the supporting services on which many of the other services depend. As well as providing food for people, cockles remove nitrogen, phosphorus and carbon from the marine environment, and have a strong cultural influence in these countries along the Atlantic coast. Preliminary economic valuation of some of these services in a European context is provided, and key knowledge gaps identified. It is concluded that the cockle has the potential to become (i) an important focus of conservation and improved sustainable management practices in coastal areas and communities, and (ii) a suitable model species to study the integration of cultural ecosystem services within the broader application of 'ecosystem services'.

1. Introduction

The coast is a major focus of human commerce, settlement and recreation globally. Coastal habitats provide many important ecosystem services including sea defence, carbon storage, nutrient regulation, and recreation (Barbier et al., 2011; Jones et al., 2011; Beaumont et al., 2014; van der Schatte Olivier et al., 2018). Coastal biodiversity plays an important role in the provision of ecosystem services, together with the natural processes of sediment transport and deposition (Mermillod-Blondin, 2011). As one component of this coastal biodiversity, the importance of shellfish for ecosystem function has long been known to marine biologists but the substantial role that shellfish play in delivering ecosystem services is increasingly recognised by other research communities (Smaal et al., 2019).

In popular perception, the most prominent ecosystem service provided by bivalve shellfish is food production, with the largest share of global production in Asia (van der Schatte Olivier et al., 2018). However, studies are now quantifying many other equally, or more,

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important ecosystem services provided by shellfish. These include non-food provisioning services such as use of shell for ornaments, poultry grit and in construction (Kelley, 2009; Morris et al., 2018; van der Schatte Olivier et al., 2018). Regulating services include removal of nutrients from coastal waters, mitigating disease, and increasing seabed roughness, and modifying sediment erodibility. In some areas, the potential for the removal of nitrogen and phosphorus from eutrophic coastal waters has been turned into a transacted ecosystem service through various forms of Payments for Ecosystem Services schemes. In the Baltic Sea, blue mussels (*Mytilus edulis*) have been used to remove nutrients as an alternative nature-based solution to upgrading a tertiary sewage plant (Petersen et al., 2014), while in Chesapeake Bay in the USA, restored Eastern (American) oyster *Crassostrea virginica* reefs in coastal waters are used to remove nutrients of agricultural origin draining from inland catchments (Rose et al., 2014). Cultural services are also provided by shellfish, with many examples of imagery and references to shells in cultures throughout the world (Duncan and Ghys, 2019; van der Schatte Olivier et al., 2018). However, cultural services or 'non-material benefits' (Díaz et al., 2015) remain a particular challenge to quantify and assess (Chan et al., 2012), and research on cultural services remains a tiny fraction of that undertaken for the other ecosystem services (Fish et al., 2016; García Rodrígues et al., 2017).

Key to providing these services are the underpinning natural functions performed by shellfish. Shellfish play a vital role as an ecosystem engineer, controlling or influencing processes such as bioturbation and water filtration which underpin marine food webs and biodiversity, and which drive biogeochemical cycling, and modify sediment erodibility. Shellfish also provide structural habitat which supports a wide range of other species. Although well known in the traditional ecological literature, the role of these supporting functions is rarely assessed within an ecosystem services framework, and so far the majority of the work in this area has been conducted on only a single shellfish species, the Eastern oyster in the USA (Peterson et al., 2003).

Recent studies have assessed (Clements and Comeau, 2019; Coen et al., 2007; Gentry et al., 2019; Grabowski and Peterson, 2007) and valued (van der Schatte Olivier et al., 2018) the benefits of shellfish ecosystem services at a range of scales. They show that some of the non-market values are potentially worth at least 50% in addition to the global production value, and recognise that the true non-market values are likely to be much higher but are not easily quantified. However, these studies have focused almost exclusively on cultured shellfish species for example Pacific oysters *Crassostrea gigas* in the UK (Herbert et al., 2012) and blue mussels in Sweden (Lindahl et al., 2005). The role of wild-harvested species such as the common cockle *Cerastoderma edule* have largely been ignored. The ways in which non-cultured species contribute to ecosystem services can be similar to those of cultured species, for example in nitrogen and phosphorus removal, but differ in other important ways. Cockles are an in-faunal species and do not form biogenic reefs in the same way that epifaunal species like oysters and mussels do, therefore the structural role they play in habitat modification differs considerably from those species. Cockles are also a natural resource that is harvested rather than farmed or cultured from spat (juveniles) (Pronker et al., 2013). Thus, the amount of human-derived capital required to access the services (Jones et al., 2016) is typically lower for wild shellfish than for cultured species, i.e. the relative contribution of natural capital is higher. In addition, harvesting methods for wild shellfish such as cockles often retain older traditions which have been lost in the more advanced production methods of cultured species, increasing the connections to cockle harvesting among local communities.

The common cockle is one of the main non-cultured bivalve species harvested in western European waters. The species is widely distributed in the Atlantic, extending from northern Europe (Norway, Russia) to the coasts of West Africa (Senegal) (Hayward and Ryland, 1995), making them a useful model species for this study. Cockles are one of the most abundant mollusc species in European bays and estuaries where population densities of 10,000 per m^2 have been recorded (Tyler-Walters, 2007). Animals mature when reaching ca. 20 mm shell length, have a 1–2 year generation time, and live up to 10 years in some habitats but more commonly to 2–6 years (Malham et al., 2012).

Therefore, in this paper we conduct an assessment of the ecosystem services of the common cockle *Cerastoderma edule* (hereafter 'cockle' or *C. edule* as appropriate), a non-cultured shellfish species. The aim of the study was to collate evidence and data, and conduct a preliminary valuation analysis, to demonstrate the substantial role played by the common cockle, and provide this information in such a way to allow others to build on this in further ecosystem service assessments. We synthesise data and information from throughout the geographical range of the species and in particular from five countries along the Atlantic European coast with a long history of cockle fisheries: Portugal, Spain, France, Ireland, and the United Kingdom (Wales). We first discuss the cockle as an ecosystem engineer, and its role in the supporting services on which many of the other services depend. Data on provisioning, regulating and cultural services are then collated and quantified as far as possible. The data synthesis underpins a valuation of some of these services in a European context. The paper concludes with a discussion of key knowledge gaps.

2. Material and methods

The study was conducted through a series of workshops and virtual meetings with participants from the five countries. Participants were natural scientists, economists, NGOs, and representatives of regulatory bodies and cockle fisheries. These meetings were part of the EU's Interreg Atlantic Area Programme, under the project 'Co-operation for restoring cockle shellfisheries and its ecosystem services in the Atlantic Area' (COCKLES, EAPA_458/2016), co-funded through the European Regional Development Fund (ERDF). Through these meetings and subsequent work we synthesised primary and published data that quantify the supporting, provisioning, regulating and cultural services, to allow upscaling and valuation of the services provided. The aim of this exercise was not to undertake a systematic review focused on a single topic. That would be both inappropriate and unfeasible for such a wide-ranging study. Neither was the aim to create an exhaustive literature review of the biology and ecological functions associated with the common cockle. Instead the aim was to summarise key evidence which describes the ecosystem services provided by cockles, in discussion with experts from multiple disciplines among five European countries. Evidence was collated from the scientific literature from databases including web of knowledge and Google Scholar, and from grey literature. Search terms included different scientific and vernacular names for cockle and synonyms for the functions and services they perform. From the studies identified through literature searches we selected those which allowed quantification of the function, giving greater emphasis to review studies and to field studies over laboratory studies. For cultural services, evidence was primarily derived in workshop settings and in follow-up activities with in-country teams. Numerous examples of cultural ecosystem services were collated, but it was difficult to quantify these and they were not valued due to recognised challenges in quantifying these services. The Common International Classification of Ecosystem Services (CICES v5.1) provides the structural basis for the quantification and analysis of final ecosystem services in this study (Haines-Young and Potschin, 2018). Final services are components of nature, directly enjoyed, consumed, or used to yield human well-being (Boyd and Banzhaf, 2007), as distinct from intermediate services which are broadly equivalent to the ecological functions or processes which underpin the final services. We supplement the CICES descriptions with synonymous descriptions to aid understanding where necessary, especially for supporting services which are not featured in CICES.

Valuation followed methods in van der Schatte Olivier et al. (2018). Data on meat yield were obtained from the Solway cockle fishery (18%, Scottish Government, 2015). The dry weight of meat was calculated using a drying factor of 8.7 (Ricciardi and Bourget, 1998) and the shell weight calculated using a condition index formula (Brock and Wolowicz, 1994) where shell weight = [meat dry weight x 100]/6.7. Tonnages of *C. edule* harvested were obtained from FAO data (http://www.fao.org/fishery/statistics/global-capture-production/query/en). Comparable harvest data were not available for Norway or The Netherlands; mechanical dredge harvesting of cockles in The Netherlands is currently suspended. Economic values were estimated for those services that are easily quantified: cockle meat, nutrient (N and P) removal in tissue and shell (using average valuations taken from studies comparing the cost of point source removal of these nutrients), and the use of cockle-shell waste as aggregate. All economic values are expressed as US dollars (USD/US$, 2017 values). Economic values were adjusted to account for inflation to 2017 and converted to USD using purchasing power parities (PPPs) (Hamadeh et al., 2017). The value of cockle meat was calculated by taking values from Marine Management Organisation (2017) for landed cockles, these were converted to US$ and using the meat yield data, calculated the value of cockle meat at an average of $3583 (range: $2827-4303) per tonne. The value of nitrogen removal were the mean values for point source removal of one tonne of nitrogen, calculated using values from Beseres Pollack et al. (2013) and Newell et al. (2005) at an average of $20,023 (range: $8996–31,050 t^{-1}). The value of phosphorus removal - the mean values for point source removal of one tonne of phosphorus – was calculated using values from Molinos-Senante et al. (2011) at an average of $35,840 (range: $13,118–58,561 t^{-1}). The value of cockle shell aggregate was calculated from Morris et al. (2018) at an average of $1138 (range: $538–1738 t^{-1}).

3. Results and discussion

3.1. Supporting services

Here, we describe here the basic underlying processes and functions performed by cockles as supporting services (cf. Northern Economics, 2009). These are not final services themselves (Bateman et al., 2011), but underpin the full range of other ecosystem services, including the alteration of energy flows and nutrient cycling at an ecosystem scale. Supporting services described here are water filtration, perturbation and alteration of sediment properties, biogeochemical cycling, habitat creation and biodiversity support.

3.1.1. Water filtration

Cockles are suspension feeding bivalves, consuming minute particulate matter suspended in the water column, which includes both living organisms (e.g. plankton) and non-living material (such as plant debris or suspended soil particles), together known as seston. The filtration power of bivalves has been shown to improve water quality by decreasing turbidity and removing nutrients (van der Schatte Olivier et al., 2018; McLeod et al., 2019). Two functions are differentiated: (i) the rate at which water is transported through the gills (pumping or filtration rate), and (ii) the rate at which seston particles are captured (clearance rate).

In general, filtration rate in cockles increases with body size (as a result of the associated increase in gill surface area), however rates vary depending on food availability, temperature and physiological (mainly reproductive) conditions (Iglesias et al., 1996 Smaal et al., 1997). The volume of water filtered increases rapidly with increasing proportion of particulate inorganic matter up to a concentration of about 300 mg/L, above which it remains constant as long as the proportion of seston particles is high (Navarro and Widdows, 1997). Filtration rates are highest in the temperature range 8–20 °C (Brock and Kofoed, 1987), particularly in spring to provide the amount of energy required for the development of gonads (Newell and Bayne, 1980), while cockles strongly reduce their filtration activity at low temperatures (<8 °C), even when food is available (Smaal et al., 1997). Filtration rate is largely independent of current speed, except below 5 cm/s when rates are lower (Widdows and Navarro, 2007). Filtration rates reviewed in Riisgård (2001) cites a filtration rate (F, in Lh^{-1}) for cockles of $F = 11.60\ W^{0.70}$, where W is tissue dry weight (g).

Standardised clearance rates were calculated by Cranford et al. (2011), who standardised them by body weight (to a 1g animal, and using a standardised *b* coefficient of 0.58) or shell length (to a 60 mm animal, and using a standardised *b* coefficient of 1.8). For *C. edule*, the mean (±2 SE) clearance rate based on body weight was 3.58 (±0.38) $Lg^{-1}h^{-1}$. Mean clearance rates standardised by shell length were 6.03 (±0.81) $Lind^{-1}h^{-1}$. Cranford et al. (2011) stress the importance of quantifying local site-specific rates at relevant times of year to the specific application of the data, noting studies which show that *in-situ* activity rates in mussels range from 42 to 55% of the maximum values observed in laboratory experiments.

3.1.2. Perturbation and alteration of sediment properties

From a functional point of view, cockles are classified as surficial biodiffusers, inducing diffusive-like sediment reworking and bio-irrigation processes within the uppermost few centimeters of the sediment column (Norkko and Shumway, 2011; Kristensen et al., 2012). The burrowing and locomotion activities of cockles induce a continuous mixing of particulate material, whilst their filtration and valve movements enhance pore water displacement and solute exchanges across the sediment-water interface (Mermillod-Blondin et al., 2005). However, the activity of cockles on sediment bed properties is complex and can either increase (e.g. Andersen et al., 2010) or decrease (e.g. Ciutat et al., 2006, 2007; Li et al., 2017) sediment stability.

On one hand, cockles act through their bioturbation activity, as sediment destabilizers. By mechanically altering the physical properties of the sediment matrix (i.e. decreasing compaction and cohesiveness while increasing bed roughness), cockles can drastically lower erosion thresholds and increase erodibility (Ciutat et al., 2006, 2007; Neumeier et al., 2006; Li et al., 2017; Liu and Su, 2017). On the other hand, by improving microbially-mediated nutrient regeneration and facilitating the development of microphytobenthic diatoms, cockles indirectly stimulate the secretion of exopolymeric substances that creates bonds between particles and thus reinforces their cohesion, contributing to sediment stability (Tolhurst et al., 2002; Meadows et al., 2012).

The effect on sediment stability is therefore substrate dependent. In fine sediments, cockle movement can disrupt cohesive sediments, especially when the mud fraction is high (>30%). By contrast, in coarse sandy sediments the biodeposit production, integration of pseudofaeces in the sand matrix and microphotobenthic (MPB) biofilm produced by a range of benthic organisms can considerably enrich the fine fraction, thereby stabilizing the non-cohesive sandy areas. The activity of cockles does not modify the erodibility of non-cohesive (sandy) sediments but it does increase the erodibility of cohesive ones - an effect which is density dependent and increases with current velocity (Rakotomalala et al., 2015; Li et al., 2017). In the longer-term, these processes lead to an increased sand content in muddy sediments, and to an increased silt content in sandy ones (Soissons et al., 2019) maintaining the sediment as a sand-mud mixture best for cockle growth.

The role of cockles as ecosystem engineers is conclusively demonstrated through large-scale manipulation experiments conducted on intertidal flats controlled by blue mussels (Donadi et al., 2013). They showed that high densities of cockles enhanced sediment stability (specifically sand rather than mud) and so are important in conserving and promoting the primary productivity of soft-bottomed intertidal ecosystems. The joint effects of coexisting engineering species, blue mussels, lugworm (*Arenicola marina*) and cockles, also determined the large-scale structure of an intertidal macrobenthic community (Donadi et al., 2015). Thus cockles clearly play a vital role in shaping natural communities, and this has implications for the ecosystem services they provide.

3.1.3. Biogeochemical cycling

In a biomanipulation experiment involving nutrient enrichment in a soft-sediment food web, Eriksson et al. (2017) showed that, as well as promoting sediment stability, cockle beds also enhanced the nutrient uptake efficiency of the biofilm. Cockles contribute to nutrient transformation and fluxes across the sediment-water interface through respiration and direct excretion of metabolic wastes (Swanberg, 1991). However, their primary influence on the biogeochemical dynamics of intertidal sediments comes through their biodeposition and bioturbation activities (Mermillod-Blondin et al., 2004; Rakotomalala et al., 2015). Cockles capture seston particles in the water column and eject substantial amounts of faeces and pseudofaeces on the sediment surface, thereby increasing the vertical downward flux of organic matter. Tightly bound in mucus, biodeposits are not easily resuspended by turbulence and thus accumulate within the surficial sediment (Widdows and Navarro, 2007). The biogenic sediment reworking induced by cockles and associated macrofaunal communities quickly incorporates this freshly sedimented organic material into deeper sediment layers, thereby fuelling the benthic microbial food web. Microbial remineralisation activities are further stimulated by bioirrigation, which increases the depth of oxygen penetration and modifies the vertical sequence of redox reactions (Aller, 1982).

Collectively, biodeposition and bioturbation processes increase the pore water concentrations of inorganic nutrients, some of which is re-released to overlying water (Karlson et al., 2007). In doing so, they increase ammonium concentrations which is the most important resource for microphytobenthic communities (Brito et al., 2010). As benthic microalgae can represent a large part of the diet of cockles (Kang et al., 1999), the stimulation of MPB production represents an indirect way of supporting their own food sources (Andersen et al., 2010; Donadi et al., 2013; Rakotomalala et al., 2015).

3.1.4. Biodiversity support

Cockles both indirectly and directly support complex food webs ranging from primary producers right up to avian and other predators. The indirect effects result from their role in sediment and nutrient processing and resuspension. The valve movements of cockles increase microphytobenthic biofilm productivity (Swanberg, 1991) and increase the resuspension rates of organic material towards the water column (Rakotomalala et al., 2015), both of which help to sustain pelagic food webs. In estuaries where blue mussels and Pacific oysters are cultivated, the dominant presence of cockles in adjacent areas are thought to contribute to increased food availability for these farmed species through resuspended microphytobenthos, consumption of which doubled in summer when cockle-dominated mollusc biomass was 20 times higher than in the spring (Ubertini et al., 2012). Through their context-specific ecosystem engineering and subsequent changes in sediment conditions, cockles have been shown to shift the functional composition of communities of infaunal species such as polychaetes, amphipods, and bivalves (Donadi et al., 2015).

Cockles are a major food source for crustaceans, fishes and wading birds, with species-specific predation varying according to cockle size. At very early stages, bivalve larvae can be ingested by filtering bivalve feeders, including adult cockles (André and Rosenberg, 1991). Post-larvae cockles (newly settled spat) are a food source for brown shrimp (*Crangon crangon*) and juvenile shore crabs (*Carcinus maenas* - see van der Veer et al., 1998; Beukema and Dekker, 2005). At sizes of 5–10 mm cockles become prey for fish, particularly European plaice (*Pleuronectes platessa*) and flounder (*Platichtys flesus* – see Möller and Rosenberg, 1983; Pihl, 1985). Larger cockles are predated by shore crabs, a range of gastropod predators and fishes (Mascaró and Seed, 2000; Morton et al., 2007) and wading birds, many of which have protected status. In Europe, the cockle is the main food supply for overwintering oystercatchers (*Haematopus ostralegus;* Bryant, 1979; Ens et al., 2004), and the presence of cockles can be a significant predictor of oystercatcher density (Van der Zee et al., 2012). In the absence of mussel beds (their main alternative food source), oystercatchers require an estimated 105–232 kg cockle flesh (wet weight) per bird per winter (Ens et al., 2004). Indeed, other birds such as eider (*Somateria mollissima*), knot (*Calidris canutus*), shelduck (*Tadorna tadorna*), curlew (*Numenius arquata*), redshank (*Tringa tetanus*), dunlin (*Caladris alpine*), sanderling (*Caladris alba*) and common gull (*Larus canus*) also eat cockles as part of a broader diet of bivalves and worms (Cadée, 1994 Bryant, 1979). Cockle availability is a key resource supporting many overwintering wader populations and the responses of oystercatchers and other species to insufficient food supplies during the overwinter period are well documented and include reduced individual body condition, increased mortality and reduced population sizes (Verhulst et al., 2004). In turn, the birds that cockles support provide ecosystems services of their own, most often explored as cultural services.

3.2. Provisioning services

The CICES provisioning services includes the Division ‘Biomass’, which includes the Group ‘Reared aquatic animals for nutrition, materials or energy’, further divided into Classes used for nutritional purposes (CICES code 1.1.6.1) or for other uses (1.1.6.2). In the following text we categorise these as use of the shellfish meat for consumption and multiple uses of shells: shell by-products, poultry grit, and use in construction.

3.2.1. Shellfish meat

Cockles are consumed for their taste and nutritional benefits and harvesting cockles is embedded deep within the history and culture of European countries. Humans have gathered cockles for consumption since at least Neolithic times (Montgomery et al., 2013). The historical importance of cockles as a food source is highlighted by their presence in many middens across Europe (e.g. Murray, 2011; Fernández-Rodríguez et al., 2014; Duarte et al., 2017). Today a multinational industry has grown around the processing and supply of cockles to markets in continental Europe, the UK and Ireland, and beyond (Table 1).

Shellfish meat is a good source of many vitamins and minerals and is low in saturated fat and high in the omega-3s DHA and EPA (Heid, 2018). The value of harvested cockles is mainly in the market value of their meat. Annual production of cockles in Europe from 2014 to 17 varied between 14,000 and 26,000 tonnes (Table 1), with production dominated by the UK, Spain, Portugal and Denmark. The Netherlands was a major producer of cockles until prohibition of cockle fishing by mechanical dredging in 2004 (Floor et al., 2013) and is now mainly a manual hand raked fishery with Marine Stewardship Council certification. The value of cockles fluctuates considerably with supply and demand, and in comparison with other shellfish species the value is low. Available data show that the price for cockles (2014–2017) averaged \$466 t^{-1} (range: \$352–541 t^{-1}), compared with \$727 t^{-1} (range: \$559–947 t^{-1}) for mussels and \$1355 t^{-1} (range: \$1145-1588 t^{-1}) for

Table 1

Annual reported European harvest (tonnes) of *Cerastoderma edule* by country for 2014–17 (data from FAO – Fisheries and Aquaculture Information and Statistics Branch, 09/08/2019, http://www.fao.org/fishery/statistics/global-capture-production/query/en). Countries are listed based on 2014 data, ranked in order of decreasing reported harvest.

Country	Year			
	2014	2015	2016	2017
UK	10,171	11,169	5036	5997
Denmark	6081	7699	5917	7924
Portugal	1991	4700	1835	5063
Spain	1195	2410	1561	2846
France	228	145	80	259
Ireland	3	0	222	441
Sweden	0	2	0	0
European Total	**19,669**	**26,125**	**14,651**	**22,530**

scallops (Marine Management Organisation, 2017).

As well as harvesting for commercial purposes, there is often a commonly accepted ‘public right’ to collect shellfish along the foreshore (Meadowcroft and Blundell, 2004) although in certain countries the amount is limited per person per day when the fishery is open. In Ireland, historically cockles were collected by the poorer in society (West et al., 1979). Cockle meat is also used by recreational anglers as an effective bait for a wide variety of sea fishes, including cod (*Gadus morhua*), flounder (*Platichthys flesus*), and dab (*Limanda limanda*) (SeaAngler, 2009).

3.2.2. Shell by-products

Cockle shells are used for a variety of purposes, including chicken grit, aggregate and for ornamental uses. Shells for these purposes are usually sourced from shellfish processing centres. Traditionally, after the meat was removed the shells were left to dry for several months before being heat treated and then crushed to the appropriate size. Modern approaches involve some pre-treatment of the shells, and the development of value-added products for construction, including mortar, aggregate, and fillers.

3.2.2.1. Poultry grit. Global poultry production has been estimated at 21 billion birds per year, producing 1.1 trillion eggs and approximately 90 million tonnes of meat annually (Blake and Tomley, 2014). Cockle shells are one of the two main shell types used in poultry grits (ground-up shell is mixed with ground granite and fed to poultry to help digestion and to provide calcium for egg shells) as their shells do not break down into sharp shards: unlike mussel and scallop shells (van der Schatte Olivier et al., 2018).

3.2.2.2. Construction and other uses. The extraction of sand can cause negative environmental impacts in terms of reduced water quality, destabilization of riparian and in-stream habitats which, in turn, destroy riverine vegetation and lead to ecological imbalance (Muthusamy et al., 2016). Considering replacement material for sand, studies have investigated the potential of cockle shell ash as a material for partial cement replacement or a filler material, with shell aggregate worth between \$240 and \$2400 t^{-1} (Morris et al., 2018). Incorporation of ground seashells resulted in reduced water demand and extended setting times of mortar, which is advantageous for rendering and plastering in hot climates. Mortar containing ground seashells also showed less shrinkage with drying and lower thermal conductivity compared to conventional cement, thereby improving the workability of rendering and plastering mortar (Hazurina Othman et al., 2013; Lertwattanaruk et al., 2012). Further, maximum concrete strength was shown to be attained with a combination of granite powder and cockle shell at 20% and 15% partial replacements of fine and coarse aggregate, respectively (Ponnada et al. (2016). The compressive strength of concrete for 28 days at these combinations was 43.7 MPa which is 44% higher than that of conventional concrete. Additionally concrete made with shell fragments as a major component of the aggregate (up to 40%), is a suitable substrate for artificial reefs, which provide effective refuge areas for marine biodiversity (Carr and Hixon, 2004; Olivia et al., 2017). Another common use for cockle shells is as an ornamental surface covering for pathways (Fig. 1a).

3.3. Regulating services

The CICES regulating services that cockles provide include the Division ‘Regulation of physical, chemical, biological conditions’, further broken down into the following Groups: ‘Atmospheric composition and conditions (2.2.6.1)’ ≈ carbon sequestration, ‘Water conditions (2.2.5.2) ≈ Salt water quality through filtration, ‘Regulation of baseline flows and extreme events’ (2.2.1.1) ≈ erosion control, ‘Pest and disease control’ (2.2.3.2) ≈ disease control. They also include the Division ‘Transformation of biochemical or physical inputs to ecosystems’, which contains the group ‘Mediation of wastes or toxic substances of anthropogenic origin by living processes’ (2.1.1) ≈ pathogen and toxin removal.

3.3.1. Carbon sequestration in shell and sediment

Bivalve aquaculture is gaining widespread attention because of its role in the carbon cycle in relation to mitigating climate change. Bivalves sequester carbon in the form of calcium carbonate via shell production (Peterson and Lipcius, 2003; Hickey, 2009). The average carbon content of a bivalve shell is 11.7%, although this varies between species. Currently there are no published figures for shell %C content of *C. edule* (van der Schatte Olivier et al., 2018). However, although shell formation fixes carbon, the biogeochemical processes involved also lead to the release of CO_2 into the atmosphere via the water column. Therefore, there is ongoing debate on whether there is a net sequestration of carbon as a result of shell formation, and whether it can be counted as an ecosystem service.

Fig. 1. Ecosystem service examples: cockles. Clockwise from top left: (a) cockle shells used on footpath on Ynys Llanddwyn, Wales © Andrew van der Schatte Olivier; (b) ‘*Ovos Moles*’ sculpture in Aveiro, Portugal © Laurence Jones; (c) ‘*The Cocklepickers*’ by Michéal McKeown in Blackrock, Co. Louth, Ireland. The sculpture overlooks Dundalk Bay, an important cockle harvesting area © Kate Mahony; (d) cockle shells as an element of a tourist trinket/souvenir © David Carss; (e) Molly Malone statue by Jeanne Rynhart in Dublin (Nol Aders, Wikimedia Commons [CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0)]e)].

3.3.2. *Nutrient removal*

Shellfish remove both nitrogen and phosphorous in a variety of ways (Carmichael et al., 2012). Cockles remove nutrients from the water column through the production of biodeposits in the form of faeces and psuedofaeces. The biodeposits increase the denitrification potential by providing anoxic environments for denitrifying bacteria (Newell et al., 2005). This microbial-facilitated process releases unreactive nitrogen gas (N_2) from the aquatic system to the atmosphere, thereby removing nitrogen from coastal waters. This is a regulating service provided *in situ*. Nitrogen and phosphorus are also taken up and used for both shell and tissue growth, and will be removed from the coastal ecosystem when animals are harvested (van der Schatte Olivier et al., 2018). To our knowledge, there is no published quantification of the nitrogen and phosphorous content of cockle shell and tissue.

3.3.3. *Erosion protection*

While cockles do not form large reefs in the same way most oyster and mussel species do, their activity can lead to increased bed stability and reduced erosion risk in sandy substrates (but see section 3.1.2 for a description of processes which have the opposite effect in fine silty sediment). The biodeposition of fine-grained material, the production of mucus and the formation of a structural layer of shells within the sediment layer are all factors which increase surficial stability, hence reducing erosional processes caused by hydrodynamic forces (Andersen et al., 2010; Eriksson et al., 2017; Soissons et al., 2019) (see more detailed description of the processes in section 3.1.2).

3.3.4. *Disease regulation*

Cockles are hosts to a wide variety of parasites and diseases (Longshaw and Malham, 2013). As with other filter and deposit feeding organisms, cockles can accumulate agents that are potentially ‘pathogenic’ (Zannella et al., 2017). This can have both positive and negative effects, either by accumulating in the cockles and thus reducing general pathogen load, or alternatively, by acting as a reservoir for subsequent infection of other species. The high levels of MPB biofilms associated with cockle beds may increase the persistence of infectious agents in the sediment. Further research is required to better estimate the positive and negative influence of bivalves on pathogen levels in the coastal environment (Zannella et al., 2017).

3.3.5. *Pathogen and toxin removal*

Harmful algal blooms in the coastal zone are regarded with some concern, as they can have direct impacts on human health, as well as the environment (Berdalet et al., 2016). Most algal toxins are relatively harmless for bivalves but they accumulate and concentrate toxic compounds that can be lethal to humans or other consumers (Anderson, 2009). The toxins do not remain indefinitely, but are eliminated at rates dependent on the physiological mechanisms of the bivalve and the type of toxin (Blanco, 2018). Modelling studies suggest that removal of harmful algae cells and cysts by shellfish can occur, but is dependent on the bivalve species and their filtering capacity (Yñiguez et al., 2018). Cockles remove significant amounts of phytoplankton biomass through filter feeding, however few studies have focused on the potential to reduce quantities of harmful algae. Furthermore, while they may provide a service in reducing the incidence or severity of algal blooms, there can be trade-offs with cockle harvest for human consumption.

3.4. *Cultural services*

The classification of cultural ecosystem services in CICES is wordy, but broadly encompasses Divisions describing direct (*in situ*) or indirect (remote) interactions with living or abiotic systems. These are further categorised into Groups which include: ‘Physical and Experiential (3.1.1)’, ‘Intellectual and Representative (3.1.2)’, ‘Spiritual or Symbolic (3.2.1)’ and other ‘non-use (3.2.2)’ interactions.

A suite of cultural services for cockles with ‘value’ to individuals and society emerged clearly during the workshops and subsequent meetings with the participants from all five countries. These included evidence of interactions with the physical landscape passing from generation to generation, and also evidence of intangible aspects of cultural behaviour (cf. Tenberg et al., 2012). They are described under the CICES group-headings below.

3.4.1. *Physical and experiential*

Perhaps the most common manifestation of this was the ubiquitous value attached to family-focused activities, where cockles formed part of a wider evocation of ‘place’ (Fish et al., 2016):

- Family holidays or day trips to the seaside
- Memories of childhood, often recreated by adults now with their own children – very often spanning several generations
- Space to play: sandy/muddy shores – shallow water, relatively safe environments, easy access
- Wide vistas of sea and sky – high visual amenity
- Collecting, cooking and eating cockles as a family/summer activity

Alongside non-commercial (‘family’) harvesting conducted as part of a social activity, there was also evidence for strongly traditional cultural activities in relation to small-scale commercial harvesting of cockles (often referred to as ‘gathering’). These traditional practices were widespread, for example cockles have been gathered in Wales (Jenkins, 1984) and Galicia (Villalba et al., 2014) for centuries - providing much-needed employment (very often for women) and cheap food. In Galicia, there is a local movement to register cockle gathering as a protected ‘cultural landscape’ status in the Ría de Noia.

3.4.2. *Intellectual and representative*

The largest body of evidence fell under this category, encompassing art, architecture, and advertising. Cockles and cockle harvesting are represented in both historical and contemporary art. One of the earliest records of cockles in European human culture relates to *Cardium* pottery. This is a Neolithic (6400 BC - 5500 BC) decorative style of pottery derived from imprinting clay with the shells of cockles (formerly named *Cardium edule*). This pottery style gives its name to the main Mediterranean Neolithic culture – ‘Cardial’ culture – which extended from the Adriatic Sea to the Atlantic coasts of France, the Iberian Peninsula and Morocco (see for example, Spataro, 2009).

Modern examples of art include a sculpture in Aveiro, Portugal, by the artist Albano Martins. The sculpture embodies a giant cockle shell (Fig. 1b) as an homage to Ovos Moles de Aveiro ("soft eggs from Aveiro") a local sweet delicacy made from egg yolks and sugar, frequently put inside small rice paper casings in sea-themed shapes such as shells. The artist Raphael Bordallo Pinheiro (1846–1905) was one of the most influential people in nineteenth century Portuguese culture, associated with caricature and artistic ceramics. He was responsible for an internationally recognised cockle-shaped piece produced by the ceramics company Bordallo for decorative and advertising purposes.

In Spain there is a rich tradition of cockles and other shellfish being represented in fine art during the 20th Century, particularly in relation to harvesters (often women) and specific estuarine habitats with shifting land- and seascapes. A number of Spanish sculptors have depicted cockle fishers, either as monuments to them and their activities or in the form of individuals representing ‘place’ in terms of their clothing and harvesting tools, ‘status’ in terms of their means of livelihood, and ‘freedom’ in terms of their activity and relation to nature. Evoking coastal landscapes and activities, cockle fishing is also represented in French, Irish and British art works, including in Ireland a recent (2018) sculpture called ‘*The Cocklepickers*’ celebrated the historic culture of local cockle picking (Fig. 1c). Possessing or viewing such art works feeds into, and is deeply interwoven with, notions and memories of family-focused activities with cockles evoking a strong sense of ‘place’ (Fish et al., 2016).

As well as the examples described above, the workshop also produced other examples of cultural services provided by cockles. For example, their shells are an element of tourist trinkets and souvenirs in many coastal towns and villages (Fig. 1d). Collecting seashore shells is a worldwide leisure activity, and is the basis of the scientific discipline of malacology. They are used as examples of anatomy and invertebrate structure in zoological textbooks; the presence of shells in the fossil record informs evolutionary studies; and their mineral content can reveal past climatological events and act as long-term archives.

3.4.3. *Spiritual and symbolic*

Cockles in folklore are difficult to classify, forming part of both inspirational but also symbolic values. Here we chose to group them under the latter, due to their role in defining national identity. Perhaps the most widely known example is that presented in the Irish (but also claimed as originally Scottish) folk song (ca. 1870s–1880s) celebrating the life of Molly Malone (see Murphy, 1992, see Fig. 1e). The song (variously titled: “Molly Malone”, “Cockles and Mussels” or “Dublin’s Fair City”) tells of a fishmonger who plied her trade on the streets. The persona of Molly Malone and her cry of “Cockles and mussels, alive, alive oh!” have become world famous. Set in Dublin, the song has become the unofficial anthem of Ireland sung regularly by crowds at international sporting events. Other human-associated links with cockles in the form of shell fragments are found throughout Ireland in archaeological remains from tombs (O’Nualláin, 1989), ringforts and monasteries (Murray, 2011).

3.4.4. *Other non-use values*

One service rarely discussed is the role of biotic/abiotic inspiration in language. Cockles provide some interesting examples, with some unusual alternative meanings in slang and vernacular language in several countries. In Cornwall, south west England, cockle gathering or ‘raking’ occurs each spring as part of the Christian Easter celebrations and is called “trigging” in the local dialect. This word is also slang for female masturbation (see lyrics for OutKast song ‘Caroline’). In Portugal, *berbigão* - the word for cockle - is used as a synonym for the clitoris in vernacular language, presumably as a result of similarities in appearance between the shucked bivalve and the human female sex organ.

Besides cockles, but ecologically dependent on them (see section 2.5), shorebirds are also observed and used as artistic and spiritual inspiration by millions of people around the globe (Whelan et al., 2015) and the large flocks of oystercatchers, red knot and other cockle-feeding birds are an integral part of the cultural experience of a visit to the coast. The indirect value of cockles to the bird watching economy is difficult to quantify but undoubtedly contributes to visitor numbers in coastal areas.

3.5. *Preliminary valuation of ecosystem services from cockles in Europe*

The physical quantities of nutrients (nitrogen and phosphorous) removed from shell and tissue, the tonnage of meat and available shell aggregate are shown in Table 2 and the potential economic value in Table 3. The largest non-food value is ascribed to shell waste. Annually 5543 tonnes of cockle shell are produced, having the potential to be used as aggregate, worth $6.3 million ($3.0 million–9.6 million). Nutrient remediation has a lower value, predominantly for nitrogen removal, which could increase the value of the cockle industry by approximately $1.2 million. If there were ready markets for all these services, the potential value of C. *edule* would be an additional $7.5 million ($3.5 million-$11.5 million) annually.

4. Concluding remarks

The cockle is an important commercial and cultural species in those areas where it is common. This study suggests that the value and ecosystem importance of cockles is often overlooked, compared with other commercial bivalve species. Whilst often considered the ‘poor relation’ of mussels and oysters, cockles contribute significantly to the coastal systems where they occur. As an ecosystem engineer, the species is very effective at increasing the productivity of sedimentary habitats, and they directly provide a food source for predators, thereby supporting the diversity and productivity of a wide range of other species. Cockles are a key species, which provide regulating ecosystem services such as water purification and eutrophication control. They could also play a role in reducing bed erosion in areas dominated by sandy sediments although these effects have not been tested at a landscape scale, and further research is required to demonstrate the service of erosion protection *in situ*.

A second point to note is the wider societal value of cockles and the positive implication for their sustainable management through acknowledgement of the diverse cultural ecosystem services associated with them. There is a clear link between cockle harvesting and the historically less affluent coastal communities (acknowledged in popular songs and poems of oral tradition for example), and this was a common feature of the cultural footprint of cockles in all areas covered by the present work. Such clear cultural associations also suggest that the cockle may be a useful species to include in future exploration of cultural ecosystem services in coastal areas. Despite difficulties in quantitatively assessing cultural ecosystem services, they are often more directly and intuitively recognised by local stakeholders. Some studies suggest that the perception of value and the willingness to pay for environmental protection and greater management costs is higher in coastal indigenous communities than inland, when compared with other trade-offs (Kirsten et al., 2015). Therefore, the work around cultural ecosystem services in cockles could facilitate both the adoption of measures for a more sustainable approach to their management and more effective communication of the importance of this coastal resource.

Against a background where little attention is usually given to cultural ecosystem services, there are calls to fill these knowledge gaps by linking ecosystem services research with cultural landscape research, through the common interest in the demands that people place on, and the benefits derived from, landscapes and ecosystems (Schaich et al., 2010). Landscapes – or seascapes – have been shown to provide a useful conceptual bridge between ecosystem functions and cultural values in the ecosystem (e.g. Gee and Burkhard, 2010) as clear relationships between them are inherently difficult to establish (Vejre et al., 2010). The physical landscape is a foundation but intangible value is assigned by adding cognitive and imaginative overlays to this environment (Brady, 2003; see also Fischer and Hasse, 2001), the nature of which depends on

Table 2
Estimated potential amount (t) of constituents within the reported European *C. edule* catch (2015).

Country	Total tonnage landed	Meat	Weight of shell	Nitrogen remediated	Phosphorus remediated
Denmark	5917	1065	1827	17.3	1.7
France	1896	341	585	5.5	0.6
Ireland	222	40	69	0.6	0.1
Italy	56	10	17	0.2	0.0
Portugal	1958	352	605	5.7	0.6
Spain	2623	472	810	7.7	0.8
United Kingdom	5037	907	1555	14.7	1.5
Total	18,027	3188	5469	51.7	5.1

Table 3
Estimated potential value [mean (range)] of shellfish ecosystem services for the reported European *C. edule* catch (2015). Units are x100,000 US$.

Country	Meat	Shell as aggregate	Nitrogen remediation	Phosphorus remediation	Total value of ecosystem services
Denmark	$38.1 (30.1–45.8)	$21.1 (10.0–32.2)	$3.5 (1.6–5.4)	$0.6 (0.2–1.0)	$63.3 (41.9–84.4
France	$12.2 (9.6–14.7)	$6.8 (3.2–10.3)	$1.1 (0.5–1.7)	$0.2 (0.1–0.3)	$20.3 (13.4–27.0)
Ireland	$1.5 (1.1–1.8)	$0.8 (0.4–1.2)	$0.1 (0.1–0.2)	$0.0 (0.0–0.0)	$2.4 (1.6–3.2)
Italy	$0.4 (0.3–0.4)	$0.2 (0.1–0.3)	$0.0 (0.0–0.1)	$0.0 (0.0–0.)	$0.6 (0.4–0.8)
Portugal	$12.7 (10.0–15.2)	$7.0 (3.3–10.7)	$1.1 (0.5–1.8)	$0.2 (0.1–0.3)	$21.0 (13.9–28.0)
Spain	$17.0 (13.3–20.3)	$9.3 (4.4–14.3)	$1.5 (0.7–2.4)	$0.3 (0.1–0.4)	$28.1 (18.5–37.4)
United Kingdom	$32.5 (25.6–39.0)	$17.9 (8.5–27.4)	$2.9 (1.3–4.6)	$0.5 (0.2–0.9)	$53.8 (35.6–71.9)
Total	$114.3 (90.2–137.2)	$63.1 (29.8–96.3)	$10.3 (4.6–16.0)	$1.8 (0.7–3.0)	$189.5 (125.3–252.6)

prior experience, knowledge, imagination, expectations and tradition. In this context, so-called cultural heritage values (Millennium Ecosystem Assessment: MEA, 2005) are important to consider in relation to ecosystem management because societies tend to place high value on the maintenance of historically important landscapes (cultural landscapes) or culturally significant species (Tenberg et al., 2012). Cockles are strongly associated with physical landscapes - the intertidal reaches of muddy and sandy shores, often in estuarine areas - and are usually the culturally significant species there.

The 'humble' cockle thus has the potential to become not only an important focus of conservation and for improved sustainable management practices in relatively economically-deprived coastal areas and communities, but also a model study species for the better integration of cultural ecosystem services within the broader paradigm and application of 'ecosystem services' as a way of conceptualising the environment. In addition, the more easily quantified regulating services such as nitrogen and phosphorus removal presented here, can be used in other coastal and restoration studies to evaluate the wider benefits of cockles beyond their simple production value for cockle meat.

Declaration of competing interest

None.

CRediT authorship contribution statement

David N. Carss: Writing - original draft. **Ana C. Brito:** Writing - original draft. **Paula Chainho:** Writing - original draft. **Aurélie Ciutat:** Writing - original draft. **Xavier de Montaudouin:** Writing - original draft. **Rosa M. Fernández Otero:** Writing - original draft. **Mónica Incera Filgueira:** Writing - original draft. **Angus Garbutt:** Writing - original draft. **M. Anouk Goedknegt:** Writing - original draft. **Sharon A. Lynch:** Writing - original draft. **Kate E. Mahony:** Writing - original draft. **Olivier Maire:** Writing - original draft. **Shelagh K. Malham:** Writing - original draft. **Francis Orvain:** Writing - original draft. **Andrew van der Schatte Olivier:** Writing - original draft. **Laurence Jones:** Writing - original draft.

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References

Aller, R.C., 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall, Pl, Tevesz, M.J.S. (Eds.), Animal-sediment Relations-The Biogenic Alteration of Sediments. Topics in Geobiology Plenum Press, New York (Plenum Press, New York).

Anderson, D.M., 2009. Approaches to monitoring, control and management of harmful algal blooms (HABs). Ocean Coast Manag. 52, 342–347.

Andersen, T.J., Lanuru, M., van Bernem, C., Pejrup, M., Rirthmueller, R., 2010. *In situ* erosion measurements on fine-grained sediments from the Bay of Fundy. Mar. Geol. 108, 175–196.

André, C., Rosenberg, R., 1991. Adult–larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria.* Mar. Ecol. Prog. Ser. 71, 227–234.

Barbier, E.B., Hacker, S.D., Kennedy, K., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem servivces. Ecol. Monogr. 81 (2), 169–193.

Bateman, I.J., Mace, G.M., Fezzi, C., Atkinson, G., Turner, K., 2011. Economic analysis for ecosystem service assessments. Environ. Resour. Econ. 48, 177–218.

Beaumont, N.J., Jones, L., Garbutt, A., Hansom, J.D., Toberman, M., 2014. The value of carbon sequestration and storage in UK coastal habitats. Estuar. Coast Shelf Sci. 137, 32–40. https://doi.org/10.1016/j.ecss.2013.11.022.

Berdalet, E., Fleming, L.E., Gowen, R., Davidson, K., Hess, P., Backer, L.C., Moore, S., Hoagland, P., Enevoldsen, H., 2016. Marine harmful algal blooms, human health and wellbeing: challenges and opportunities in the 21st century. J. Mar. Biol. Assoc. U. K. 96, 61–91.

Beseres Pollack, J., Yoskowitz, D., Kim, H.C., Montagna, P.A., 2013. Role and value of nitrogen regulation provided by oysters (*Crassostrea virginica*) in the mission-aransas estuary, Texas, USA. PLoS One 8. https://doi.org/10.1371/journal.pone.0065314.

Beukema, J.J., Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar. Ecol. Prog. Ser. 287, 149–167.

Blake, D.P., Tomley, F.M., 2014. Securing poultry production from the ever-present Eimeria challenge. Trends Parasitol. 30 (1), 12–19. https://doi.org/10.1016/j.pt.2013.10.003.

Blanco, J., 2018. Accumulation of dinophysis toxins in bivalve molluscs. Toxins 10, 453.

Boyd, J., Banzhaf, S., 2007. What are ecosystem services? The need for standardized environmental accounting units. Ecol. Econ. 63, 616–626.

Brito, A.C., Newton, A., Tett, P., Fernandes, T.F., 2010. Sediment and water nutrients and microalgae in a coastal shallow lagoon, Ria Formosa (Portugal): implications for the water framwork directive. J. Environ. Monit. 12, 318–328.

Brady, E., 2003. Aesthetics of the Natural Environment. Edinburgh University Press, Edinburgh.

Brock, V., Kofoed, L.H., 1987. Species specific irrigatory efficiency in *Cardium* (Cerastoderma) *edule* (L.) and *C. lamarcki* (Reeve) responding to different environmental temperatures. Biol. Oceanogr. 4 (3), 211–226. https://doi.org/10.1080/01965581.1987.10749491.

Brock, V., Wolowicz, M., 1994. Compositions of European population of the cerastoderma complex based on reproductive physiology and biochemistry. Oceanol. Acta 17, 97–103.

Bryant, D.M., 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). Estuarine. Coast. Mar. Sci. 9, 369–384.

Cadée, G.C., 1994. Eider, shelduck, and other predators, the main producers of shell fragments in the Wadden Sea: palaeoecological implications. Palaeontology 37, 181–202.

Carmichael, R.H., Walton, W., Clark, H., 2012. Bivalve-enhanced nitrogen removal from coastal estuaries. Can. J. Fish. Aquat. Sci. 69, 1131–1149. https://doi.org/10.1139/f2012-057.

Carr, M.H., Hixon, M.A., 2004. Artificial reefs: the importance of comparisons with natural reefs. Fisheries 22, 28–33. https://doi.org/10.1577/1548-8446(1997)022<0028:artioc>2.0.co;2.

Chan, K.M.A., Satterfield, T., Goldstein, J., 2012. Rethinking ecosystem services to better address and navigate cultural values. Ecol. Econ. 74, 8–18. https://doi.org/10.1016/j.ecolecon.2011.11.011.

Ciutat, A., Widdows, J., Pope, N.D., 2007. Effect of *Cerastoderma edule* density on near-bed hydrodynamics and stability of cohesive muddy sediments. J. Exp. Mar. Biol. Ecol. 346, 114–126.

Ciutat, A., Widdows, J., Readman, J.W., 2006. Influence of cockle *Cerastoderma edule* bioturbation and tidal-current cycles on resuspension of sediment and polycyclic aromatic hydrocarbons. Mar. Ecol. Prog. Ser. 328, 51–64.

Clements, J.C., Comeau, L.A., 2019. Nitrogen removal potential of shellfish aquaculture harvests in eastern Canada: a comparison of culture methods. Aquac. Rep. 13, 100183. https://doi.org/10.1016/j.aqrep.2019.100183.

Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M.W., Posey, M.H., Powers, S.P., Tolley, S.G., 2007. Ecosystem services related to oyster restoration. Mar. Ecol. Prog. Ser. 341, 303–307. https://doi.org/10.3354/meps341299.

Cranford, P.J., Ward, J.E., Shumway, S.E., 2011. Bivalve filter feeding: variability and limits of the aquaculture biofilter (Chapter 4). In: Shumway, S.E. (Ed.), Shellfish Aquaculture and the Environment (Wiley-Blackwell, Hoboken).

Díaz, S., Demissew, S., Carabias, J., et al., 2015. The IPBES conceptual framework—connecting nature and people. Curr. Opin. Environ. Sustain. 14, 1–16. https://doi.org/10.1016/j.cosus t.2014.11.002.

Donadi, S., Westra, J., Weerman, E.J., van der Heide, T., van der Zee, E., van de Koppel, J., Olff, H., Piersma, T., van der Veer, H.W., Eriksson, B.K., 2013. Non-trophic interactions control benthic producers on intertidal flats. Ecosystems 16, 1325–1335.

Donadi, S., van der Heide, T., Piersma, T., van derr Zee, E.M., Weernam, E.J., van de Koppel, J., Olff, H., Devine, C., Hernawan, U.E., Boers, M., Planthof, L., Eriksson, B. K., 2015. Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macroinvertebrate functional groups. Oikos 124, 2502-1510.

Duarte, C., Iriarte, E., Diniz, M., Arias, P., 2017. The microstratigraphic record of human activities and formation processes at the Mesolithic shell midden of Poças de São Bento (Sado Valley, Portugal). Archaeol. Anthropol. Sci. 11 (2), 483–509.

Duncan, P.F., Ghys, A., 2019. Shells as collector's items. In: Smaal, A.C., Ferreira, J.G., Grant, J., Petersen, J.K., Strand, Ø. (Eds.), Goods and Services of Marine Bivalves. Springer International Publishing, Cham, pp. 381–411. https://doi.org/10.1007/978-3-319-96776-9_20.

Ens, B.J., Smaal, A.C., de Vlas, J., 2004. The Effects of Shellfish Fishery on the Ecosystems of the Dutch Wadden Sea and Oosterschelde. Final Report on the Second Phase of the Scientific Evaluation of the Dutch Shellfish Fishery Policy (EVA II). Alterra Rapport 1011, RIVO Rapport C056/04, RIKZ-Rapport RKZ/2004.031, Alterra (Wageningen).

Eriksson, B.K., Westra, J., van Gerwen, I., Weerman, E., van der Zee, E., van der Heide, T., van de Koppel, J., Olff, H., Piersma, T., Donadi, S., 2017. Facilitation by ecosystem engineers enhances nutrient effects in an intertidal system. Ecosphere ESA Open Access J. 8, 12.

Fernández-Rodríguez, C., Bejega-García, V., Gonzéles-Gómez-de-Agüero, E., 2014. Shellfish gathering during the iron age and roman times in the northwest of the Iberian Peninsula. In: Szabó, K., Dupont, C., Dimitrijević, V., Gastélum, L.J., Serrand, N. (Eds.), Archaeomalacology: Shells in the Archaeological Record. Archaeopress, Oxford, pp. 134–145. BAR International Series 2666.

Fish, R., Church, A., Winter, M., 2016. Conceptualising cultural ecosystem services: a novel framework for research and critical engagement. Ecosyst. Serv. 21, 208–217. https://doi.org/10.1016/j.ecoser.2016.09.002.

Fischer, L., Hasse, J., 2001. Historical and current perceptions of the landscapes in the wadden sea region. In: Vollmer, M., Guldberg, M., Maluck, M., van Marrewijk, D., Schlicksbier, G. (Eds.), Landscape and Cultural Heritage in the Wadden Sea Region—Project Report. Wadden Sea Ecosystem No. 12. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, pp. 72–97.

Floor, J.R., van Koppen, C.S.A., Dris), Lindeboom, H.J., 2013. A review of science-policy interactions in the Dutch Wadden Sea – the cockle fishery and gas exploitation controversies. J. Sea Res. 82, 165–175.

Garcia Rodrigues, J., Conides, A., Rivero Rodriguez, S., Raicevich, S., Pita, P., Kleisner, K., Pita, C., Lopes, P., Alonso Roldán, V., Ramos, S., Klaoudatos, D., Outeiro, L., Armstrong, C., Teneva, L., Stefanski, S., Böhnke-Henrichs, A., Kruse, M., Lillebø, A., Bennett, E., Belgrano, A., Murillas, A., Sousa Pinto, I., Burkhard, B., Villasante, S., 2017. Marine and coastal cultural ecosystem services: knowledge gaps and research priorities. One Ecosyst. 2, e12290 https://doi.org/10.3897/oneeco.2.e12290.

Gee, K., Burkhard, B., 2010. Cultural ecosystem services in the context of offshore wind farming: a case study from the west coast of Schleswig-Holstein. Ecol. Complex. 7, 349–358.

Gentry, R.R., Alleway, H.K., Bishop, M.J., Gillies, C.L., Waters, T., Jones, R., 2019. Exploring the potential for marine aquaculture to contribute to ecosystem services. Rev. Aquacult. 1–14. https://doi.org/10.1111/raq.12328.

Grabowski, J.H., Peterson, C.H., 2007. Restoring oyster reefs to recover ecosystem services. Theor. Ecol. Ser. 4, 281–298. https://doi.org/10.1016/S1875-306X(07)80017-7.

Haines-Young, R., Potschin, M.B., 2018. Common International Classification of Ecosystem Services (CICES) V5.1 and Guidance on the Application of the Revised Structure.

Hamadeh, N., Mouyelo-Katoula, M., Konijn, P., Koechlin, F., 2017. Purchasing power parities of currencies and real expenditures from the International Comparison Program: recent results and uses. Soc. Indicat. Res. 131, 23–42. https://doi.org/10.1007/s11205-015-1215-z.

Hayward, P.J., Ryland, J.S., 1995. Handbook of the Marine Fauna of North-West Europe. Oxford University Press, Oxford, p. 812.

Hazurina Othman, N., Hisham Abu Bakar, B., Mat Don, M., Azmi Megat Johari, M., 2013. Cockle shell ash replacement forcement and filler in concrete. Malays. J. Civ. Eng. 25, 201–211. https://doi.org/10.11113/MJCE.V25N2.303.

Heid, M., 2018. Is shellfish healthy? Here's what the experts say. *Time* [online] Available at: http://time.com/5341293/is-shellfish-healthy/. Accessed 21 Feb. 2019.

Herbert, R.J., Roberts, C., Humphreys, J., Fletcher, S., 2012. The Pacific Oyster (*Crassostrea gigas*) in the UK: Economic, Legal and Environmental Issues Associated with its Cultivation, Wild Establishment and Exploitation. Report to Shellfish Association of Great Britain.

Hickey, J.P., 2009. Carbon sequestration potential of shellfish. Available from: URL. www.thefishsite.com/articles/615/carbon-sequestationpotential-of-shellfish. accessed 09 August 2019.

Iglesias, J.I.P., Urrutia, M.B., Navarro, E., Alvarez-Jorna, P., Larretxea, X., Bougrier, S., Heral, M., 1996. Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition. J. Exp. Mar. Biol. Ecol. 197 (1), 121–143.

Jenkins, J.G., 1984. Cockles and Mussels: Aspects of Shellfish-Gathering in Wales. National Museum of Wales (Welsh Folk Museum) pp32, Cardiff.

Jones, M.L.M., Angus, S., Cooper, A., Doody, P., Everard, M., Garbutt, A., Gilchrist, P., Hansom, G., Nicholls, R., Pye, K., Ravenscroft, N., Rees, S., Rhind, P., Whitehouse, A., 2011. Coastal margins [chapter 11]. In: UK National Ecosystem Assessment. Understanding Nature's Value to Society. Technical Report, pp. 411–457. Cambridge, UNEP-WCMC.

Jones, L., Norton, L., Austin, Z., Browne, A.L., Donovan, D., Emmett, B.A., Grabowski, Z. J., Howard, D.C., Jones, J.P.G., Kenter, J.O., Manley, W., 2016. Stocks and flows of natural and human-derived capital in ecosystem services. Land Use Pol. 52, 151–162.

Kang, C.K., Sauriau, P.G., Richard, P., Blanchard, G.F., 1999. Food sources of the infaunal suspension-feeding bivalve *Cerastoderma edule* in a muddy sandflat of Marennes-Oléron Bay, as determined by analyses of carbon and nitrogen stable isotopes. Mar. Ecol. Prog. Ser. 187, 147–158.

Karlson, K., Bonsdorff, E., Rosenber, R., 2007. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. Ambio 36, 161–167.

Kelley, K.N., 2009. Use of Recycled Oyster Shells as Aggregate for Previous Concrete. MSC Thesis. University of Florida, Gainesville, FLA, p. 64, 64.

Kirsten, L.L., Oleson, M.B., Brander, L.M., Oliver, T.A., van Beek, I., Zafindrasilivonona, B., van Beukering, P., 2015. Cultural bequest values for ecosystem service flows among indigenous Fishers: a discrete choice experiment validated with mixed methods. Ecol. Econ. 114, 104–116. https://doi.org/10.1016/j.ecolecon.2015.02.028.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G. T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446, 285–302.

Lertwattanaruk, P., Makul, N., Siripattarapravat, C., 2012. Utilization of ground waste seashells in cement mortars for masonry and plastering. J. Environ. Manag. 111, 133–141. https://doi.org/10.1016/j.jenvman.2012.06.032.

Lindahl, O., Hart, R., Hernroth, B., Kollberg, S., Loo, L.O., Olrog, L., Rehnstam-Holm, A. S., Svensson, J., Svensson, S., Syversen, U., 2005. Improving marine water quality by mussel farming: a profitable solution for Swedish society. Ambio 34 (2), 131–138. https://doi.org/10.1639/0044-7447(2005)034[0131:imwqbm]2.0.co;2.

Li, B., Cozzoli, F., Soissons, L.M., Bouma, T.J., Chen, L., 2017. Effects of bioturbation on the erodibility of cohesive versus non-cohesive sediments along a current-velocity gradient. J. Exp. Mar. Biol. Ecol. 496, 84–90.

Liu, H., Su, J., 2017. Vulnerability of China's nearshore ecosystems under intensive mariculture development. Environ. Sci. Pollut. Control Ser. 24, 8957–8966.

Longshaw, M., Malham, S.K., 2013. A review of the infectious agents, parasites, pathogens and commensals of European cockles (*Cerastoderma edule* and *C. glaucum*). J. Mar. Biol. Assoc. UK 93, 227–247.

Malham, S.K., Hutchinson, T.H., Longshaw, M., 2012. A review of the biology of European cockles (*Cerastoderma* spp.). J. Mar. Biol. Assoc. UK 92, 1563–1577.

Marine Management Organisation, 2017. UK Seas Fisheries Statistics 2017. A National Statistics Publication.

Mascaró, M., Seed, R., 2000. Foraging behavior of *Carcinus maenas* (L.): comparisons of size-selective predation on four species of bivalve prey. J. Shellfish Res. 19, 283–291.

McLeod, I.M., zu Ermgassen, P.S.E., Gillies, C.L., Hancock, B., Humphries, A., 2019. Chapter 25 – can bivalve habitat restoration improve degraded estuaries? Coasts Estuar. Future 427–442.

Meadows, P.S., Meadows, A., Murray, J.M.H., 2012. Biological modifiers of marine benthic seascapes: their role as ecosystem engineers. Geomorphology 157–158, 31–48.

Meadowcroft, J., Blundell, J., 2004. The Morecambe Bay cockle pickers: market failure or government disaster? Econ. Far E. Aff. 24, 69–71. https://doi.org/10.1111/j.1468-0270.2004.t01-1-00495.x.

Mermillod-Blondin, F., 2011. The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. J. North Am. Benthol. Soc. 30, 770–778. https://doi.org/10.1899/10-121.1.

Mermillod-Blondin, F., Rosenberg, R., Francois-Carcaillet, F., Norling, K., Mauclaire, L., 2004. Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquat. Microb. Ecol. 36 (3).

Mermillod-Blondin, F., Francois-Carcaillet, F., Rosenberg, R., 2005. Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experimental study. J. Exp. Mar. Biol. Ecol. 315, 187–209.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Synthesis, vol. 155. Island Press, Washington, DC.

Molinos-Senante, M., Hernández-Sancho, F., Sala-Garrido, R., Garrido-Baserba, M., 2011. Economic feasibility study for phosphorus recovery processes. Ambio 40, 408–416. https://doi.org/10.1007/s13280-010-0101-9.

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

Montgomery, J., Beaumont, J., Jay, M., Keefe, K., Gledhill, A.R., Cook, G.T., Dockrill, S. J., Melton, N.D., 2013. Strategic and sporadic marine consumption at the onset of the Neolithic: increasing temporal resolution in the isotope evidence. Antiquity 87, 1060–1072. https://doi.org/10.1017/S0003598X00049863.

Morris, J.P., Backeljau, T., Chapelle, G., 2018. Shells from aquaculture: a valuable biomaterial, not a nuisance waste product. Rev. Aquacult. 1–16 https://doi.org/10.1111/raq.12225.

Morton, B., Peharda, M., Harper, E.M., 2007. Drilling and chipping patterns of bivalve prey shell penetration by Hexaplex trunculus (Mollusca: gastropoda: Muricidae). J. Mar. Biol. Assoc. U. K. 87, 933–940.

Murphy, S., 1992. Mystery of Molly Malone. Divelina Publications, Dublin.

Murray, E., 2011. A late Mesolithic shell midden at Kilnatierny near Greyabbey, Co. Down. J. Ir. Archaeol. 20, 1–18.

Muthusamy, K., Tukimat, N., Sarbini, N.N., Zamri, N., 2016. Exploratory study on the use of crushed cockle shell as partial sand replacement in concrete. Int. J. Res. Eng. Sci. 4, 67–71. ISSN.

Navarro, J.M., Widdows, J., 1997. Feeding physiology of *Cerastoderma edule* in response to a wide range of seston concentrations. Mar. Ecol.

Neumeier, U., Lucas, C.H., Collins, M., 2006. Erodibility and erosion patterns of mudflat sediments investigated using an annular flume. Aquat. Ecol. 40, 543–554.

Newell, R.I.E., Bayne, B.L., 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium (=Cerastoderma) edule* (Bivalvia: cardiidae). Mar. Biol. 56, 11–19.

Newell, R.I.E., Fisher, T.R., Holyoke, R.R., Cornwell, J.C., 2005. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake bay, USA. In: Dame, R.F., Olenin, S. (Eds.), The Comparative Roles of Suspension-Feeders in Ecosystems. NATO Science Series IV: Earth and Environmental Series, vol. 47. Springer, Dordrecht.

Norkko, J., Shumway, S., 2011. Bivalves as bioturbators and bioirrigators. In: Shumway, S. (Ed.), Shellfish Aquaculture and the Environment: 297-317. John Wiley & Sons Ltd, Ames, Iowa.

Northern Economics, 2009. Valuation of Ecosystem Services from Shellfish Restoration, Enhancement and Management: a Review of the Literature. Report for Pacific Shellfish Institute.

Olivia, M., Oktaviani, R., Ismeddiyanto, 2017. Properties of concrete containing ground waste cockle and clam seashells. Procedia Eng. 171, 658–663. https://doi.org/10.1016/j.proeng.2017.01.404.

Ó Nualláin, S., 1989. Survey of the Megalithic Tombs of Ireland. The Stationery Office, Dublin.

Peterson, C.H., Grabowski, J.H., Powers, S.P., 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: Quantitative valuation. Mar. Ecol. Prog. Ser. 264, 249–264.

Petersen, J.K., Hasler, B., Timmermann, K., Nielsen, P., Tørring, D.B., Larsen, M.M., Holmer, M., 2014. Mussels as a tool for mitigation of nutrients in the marine environment. Mar. Pollut. Bull. 82, 137–143. https://doi.org/10.1016/j.marpolbul.2014.03.006.

Peterson, C.H., Lipcius, R.N., 2003. Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations. Mar. Ecol. Prog. Ser. 264, 297–307.

Pihl, L., 1985. Food selection and consumption of mobile epibenthic fauna in shallow marine areas. Mar. Ecol. Prog. Ser. 22, 169–179.

Ponnada, M.R., Prasad, S.S., Dharmala, H., 2016. Compressive strength of concrete with partial replacement of aggregates with granite powder and cockle shell. Malays. J. Civ. Eng. 28 https://doi.org/10.11113/mjce.v28n2.420.

Pronker, A.E., Peene, F., Donner, S., Wijnhoven, S., Geijsen, P., Bossier, P., Nevejan, M. N., 2013. Hatchery cultivation of the common cockle (*Cerastoderma edule* L.): from conditioning to grow-out. Aquacult. Res. https://doi.org/10.1111/are.12178.

Rakotomalala, C., Grangeré, K., Ubertini, M., Forêt, M., Orvain, F., 2015. Modelling the effect of *Cerastoderma edule* bioturbation on microphytobenthos resuspension towards the planktonic food web of estuarine ecosystem. Ecol. Model. 316, 155–167.

Ricciardi, A., Bourget, E., 1998. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Mar. Ecol. Prog. Ser. 163, 245–251. https://doi.org/10.3354/Meps163245.

Riisgård, H.U., 2001. On measurement of filtration rates in bivalves - the stony road to reliable data: review and interpretation. Mar. Ecol. Prog. Ser. 211, 275–291.

Rose, J.M., Bricker, S.B., Tedesco, M.A., Wikfors, G.H., 2014. A role for shellfish aquaculture in coastal nitrogen management. Environ. Sci. Technol. 48, 2519–2525. https://doi.org/10.1021/es4041336.

Schaich, H., Bieling, C., Plieninger, T., 2010. Linking ecosystem services with cultural landscape research. Gaia 19, 269–277.

Scottish Government, 2015. Solway Cockle Fishery Management Study. Marine Scotland Science, Edinburgh, UK.

SeaAngler, 2009. Sea fishing with cockles [online] Available at: https://www.seaangler.co.uk/fishing-tips/baits/articles/sea-fishing-with-cockles. Accessed 21 Feb. 2019.

Smaal, A.C., Ferreira, J.G., Grant, J., 2019. Goods and Services of Marine Bivalves. Springer. https://doi.org/10.1007/978-3-319-96776-9.

Smaal, A.C., Vonck, A.P.M.A., Bakker, M., 1997. Seasonal variation in physiological energetics of *Mytilus edulis* and *Cerastoderma edule* of different size classes. J. Mar. Biol. Assoc. U. K. 77, 817–838.

Soissons, L.M., da Conceiçâo, T.G., Bastiaan, J., van Dalen, J., Ysebaert, T., Herman, P.M. J., Cozzoli, F., Bouma, T.J., 2019. Sandification vs. muddification of tidal flats by benthic organisms : a flume study. Estuar. Coast Shelf Sci. 228 https://doi.org/10.1016/j.ecss.2019.106355.

Spataro, M., 2009. Cultural diversities; the early Neolithic in the Adriatic region and the central Balkans: a pottery perspective. In: Gheorghiu, D. (Ed.), Early Farmers, Late Foragers, and Ceramic Traditions; on the Beginning of Pottery in the Near East and Europe. Cambridge Scholars Publishing, Cambridge, pp. 63–86.

Swanberg, L.I., 1991. The influence of the filter-feeding bivalve *Cerastoderma edule* L. on microphytobenthos: a laboratory study. J. Exp. Mar. Biol. Ecol. 151, 93–111.

Tenberg, A., Fredholm, S., Eliasson, I., Knez, I., Saltzman, K., Wetterberg, O., 2012. Cultural ecosystem services provided by landscapes : assessment of heritage values and identity. Ecosyst. Serv. 2, 14–26. https://doi.org/10.1016/j.ecoser.2012.07.006.

Tolhurst, T.J., Gust, G., Paterson, D.M., 2002. The influence of an extracellular polymeric substance (EPS) on cohesive sediment stability. Proc. Mar. Sci. 5, 409–425.

Tyler-Walters, H., 2007. *Cerastoderma edule* Common cockle. In: Tyler-Walters, H., Hiscock, K. (Eds.), Marine Life Information Network: Biology and Sensitivity Key Information Reviews [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 15-03-2019]. Available from: https://www.marlin.ac.uk/species/detail/1384.

Ubertini, M., Lefebvre, S., Gangnery, A., Grangeré, K., Le Gendre, R., Orvain, F., 2012. Spatial variability of benthic-pelagic coupling in an estuary ecosystem: consequences for microphytobenthos resuspension phenomenon. PLoS One 7, e44155.

van der Schatte Olivier, A., Jones, L., Vay, L. Le, Christie, M., Wilson, J., Malham, S.K., 2018. A global review of the ecosystem services provided by bivalve aquaculture. Rev. Aquacult. https://doi.org/10.1111/raq.12301.

van der Veer, H.W., Feller, R.J., Weber, A., Witte, J.I.J., 1998. Importance of predation by crustaceans upon bivalve spat in the intertidal zone of the Dutch Wadden Sea as revealed by immunological assays of gut contents. J. Exp. Mar. Biol. Ecol. 231, 139–157.

Van der Zee, E.M., van der Heide, T., Donadi, S., Eklöf, J.S., Eriksson, B.K., Olff, H., van der Veer, H.W., Piersma, T., 2012. Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. Ecosystems 15, 664–673.

Vejre, H., Søndergaard Jensen, F., Jellesmark Thorsen, B., 2010. Demonstrating the importance of intangible ecosystem services from peri-urban landscapes. Ecol. Complex. 7 (3), 338–348.

Verhulst, S., Oosterbeek, K., Rutten, A.L., Ens, B.J., 2004. Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. Ecol. Soc. 9 (1), 17-1-17-10. [17].

Villalba, A., Iglesias, D., Ramilo, A., Darriba, S., Parada, J.M., No, E., Abollo, E., Molares, J., Carballal, M.J., 2014. Cockle *cerastoderma edule* fishery collapse in the Ría de Arousa (Galicia, NW Spain) associated with the protistan parasite *Marteilia cochilli*. Dis. Aquat. Org. 109, 55–80. https://doi.org/10.3354/dao02723.

West, A., Partridge, J., Lovitt, A., 1979. The Cockle cerastoderma edule (L.) on the South Bull, Dublin bay: population parameters and fishery potential. In: Irish Fisheries Investigations Series B, Department of Fisheries and Forestry, 1979.

Whelan, C.J., Sekercioglu, C.H., Wenny, D.G., 2015. Why birds matter: from economic ornithology to ecosystem services. J. Ornithol. 156, S227–S238.

Widdows, J., Navarro, J.M., 2007. Influence of current speed on clearance rate, algal cell depletion in the water column and resuspension of biodeposits of cockles (*Cerastoderma edule*). J. Exp. Mar. Biol. Ecol. 343, 44–51.

Yñiguez, A.T., Maister, J., Villanoy, C.L., Deauna, J.D., Peñaflor, E., Almo, A., David, L. T., Benico, G.A., Hibay, E., Mora, I., Arcamo, S., Relox, J., Azanza, R.V., 2018. Insights into the harmful algal blooms in a tropical estuary through an integrated hydrodynamic-*Pyrodinium*-shellfish model. Harmful Algae 80, 1–14.

Zannella, C., Mosca, F., Mariani, F., Franci, G., Folliero, V., Galdiero, M., Tiscar, P.G., Galdiero, M., 2017. Microbial diseases of bivalve mollusks: infections, immunology and antimicrobial defense. Mar. Drugs 15 (6). https://doi.org/10.3390/md15060182 pii: E182.