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Ecosystem services from bivalve aquaculture

Van Der Schatte Olivier, Andrew

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Ecosystem services from bivalve aquaculture

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I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

April, 2020

Summary

Bivalve shellfish aquaculture provides many benefits to society, beyond their traditional market value. This thesis reviews and collates the evidence and valuations available on the provisioning, regulating and cultural ecosystem services provided by bivalve aquaculture species. Then focuses on a UK spatial survey of the carbon (C), nitrogen (N), and phosphorus (P) removal potential of blue mussels (*Mytilus edulis*). This is supported by a study at two sites to examine temporal variation in C, N and P. Finally, a UK economic assessment of the mussel industry is carried out to look at the potential value of non-food ecosystem services.

Bivalves provide provisioning services such as meat, pearls and shell. Regulating services such as nutrient remediation, estimated to remove 49,000 tonnes of nitrogen and 6,000 tonnes of phosphorus globally. There is little evidence on the cultural services of bivalve aquaculture, but these are broad ranging, although difficult to quantify. Globally, non-food bivalve aquaculture services are worth \$6.47 billion (\$2.95 billion–9.99 billion) per annum. However, this is likely to be an underestimate of the true value of bivalve aquaculture due to knowledge gaps in the value for several key services.

There is a need to understand factors underlying spatial variation around UK. In this thesis, differences in carbon (C), nitrogen (N) and phosphorus (P) percentage content as well as the upscaled values of whole mussels are compared. Mussels were collected at sites around the UK which had a range of annual water temperatures and high and low catchment nutrient concentrations. CHN and P analysis showed that P in tissue had a significant negative relationship with mean annual seawater temperature for both rope and bottom cultured sites. Similarly, the percentage content of P in shell had a significant negative relationship with increasing salinity. Most notable was a significant difference between rope and bottom cultured mussels. Per tonne, rope culture removed significantly more C (77.52 ± 3.65 kg), N (8.50 ± 0.59 kg) and P (0.95 ± 0.07 kg) than bottom cultured (74.74 ± 0.68 kg C, 5.00 ± 0.013 kg N and 0.43 ± 0.01 kg P). However, bottom cultured mussels removed more C in shell (60.15 ± 0.77 kg) than rope culture (46.12 ± 1.69 kg) and only C trapped in shell can be regarded as a long-term store of C.

Temporal variation was investigated at two contrasting estuaries, to assess the effects of seasonality on the removal potential of mussel aquaculture. The kg of N and P tonne⁻¹ of mussels was highest before spawning at both sites. The period immediately after spawning, had the lowest levels of N and P, before the sites recovered over autumn and winter. Similar to

previous findings, the seasonal changes observed in tissue condition followed the patterns of the reproductive cycle.

Utilising the meat to shell proportions and C, N, P results from the UK spatial survey, economic analysis of four scenarios for growth and further decline of the industry were applied. Non-food ecosystem services provided are worth the equivalent of US\$20.3 million year⁻¹ in nutrient remediation and shell as aggregate, however, should there be a decrease in trade,non-food ecosystem services could decrease to only US\$4.1 million year⁻¹. Through restoration of bottom aquaculture, the associated ecosystem services, could increase to US\$37.4 million year⁻¹. Further expansion to offshore aquaculture, could increase the value of non-food ecosystem services to US\$73.7 million year⁻¹. England is estimated to spend approximately US\$3.45 billion year⁻¹ protecting the water environment through lowering input, and mitigation of historical pollution. Whilst not the complete solution, mussel aquaculture already contributes nitrogen and phosphorus reduction through the removal of these nutrients and further work is required to compare rope offshore and intertidal mussel aquaculture in more areas.

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1 General introduction

Ecosystem services are the idea that human society benefits from the environment or nature in various ways, both directly and indirectly (Lele et al., 2013). The modern-day concept emerged in the 1970s as 'environmental services' (Wilson and Matthews 1970). This was later re-named 'ecosystem services' in the mid-1980s (Ehrlich and Mooney 1983) and gained momentum from 1997 onwards (Costanza et al. 1997). The most popular current definition of ecosystem services (ES) is "the functions and products of ecosystems that benefit humans, or yield welfare to society" (MA 2005). The idea of 'natural capital' emerged and was developed by a group of environmental economists such as David Pearce and Ed Barbier and ecological economists such as Robert Costanza and Rudolf de Groot (Lele et al., 2013). The natural capital of an ecosystem is the components of natural systems that underpin the delivery of ecosystem services, that generates different kinds of benefit flows: products or goods, indirect benefits or services and pure conservation (existence or aesthetic) values (Jones et al., 2016).

While the concept of ecosystem services is a useful tool to help describe some of the ways that humans are linked to and utilise nature (Costanza et al., 2017), it is not without its problems, as the relationships between people and nature are complex and vary depending on the person placing the value on the interaction (EEA, 2015). Fundamentally the concept of ecosystem services provides a method of communicating and comparing the value of different activities, processes and functions (Costanza et al., 2017). Ecosystem services have since been used to characterise a broad range of contributions to human wellbeing, both directly or indirectly through the natural or semi-natural functions of an ecosystem (de Groot et al., 2010; Ferreira and Bricker, 2018; Filgueira et al., 2015). Typically, supporting services are classified as ecosystem services which underpin the delivery of the final services (Provisioning, Regulation and Maintenance, and Cultural), and these can be applied to most systems (Turner and Schaafsma, 2015). In 2017, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) introduced a new and closely related concept - Nature's Contributions to People (NCP), defined as 'all the positive contributions, losses or detriments, that people obtain from nature' to capture both beneficial and harmful effects of nature on people's quality of life (Kadykalo et al., 2019; Pascual et al., 2017).

Half of all aquaculture production is made up of lower trophic species, including shellfish and algae, (Science Advice for Policy by European Academies, 2017). Bivalves (primarily clams,

mussels and oysters) accounted for 16 million tonnes of coastal and marine animal aquaculture in 2015, with an estimated market value of \$17.1 billion (FAO 2016) and in the UK the farming of mussels is the largest shellfish aquaculture sector by volume. Mussel farming can be carried out by cultivation on the seabed or by using suspended culture. The first method involves locating and fishing seed mussel of around 10mm shell length from offshore beds and then relaying in a more productive, protected location, termed a 'lay' (Garen et al., 2004). In Wales, Northern Ireland, The Wash, North Norfolk and Poole Harbour mussel production is mostly made up of bottom culture, within restricted Several Order fisheries (Laing and Spencer, 2006). In suspended culture (Grant et al., 2012), the mussels are cultivated on a system of ropes and floats, where they grow until harvest 18 - 24 months later. Rope grown mussels are produced in the UK, predominantly in Scotland, but also in Cornwall, but likely represent a much smaller proportion of UK-wide mussel production than seabed culturing, although there is no published overview to validate this impression.

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 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, which include removal of nutrients from coastal waters, carbon storage, mitigating disease, increasing seabed roughness, and modifying sediment erodibility. Cultural services or 'non-material benefits' (Díaz *et al.*, 2015) remain a particular challenge to quantify and assess. Research on cultural services remains under-assessed compared to other ecosystem services (Carrs *et al.*, 2020). Cultural ecosystem services can changes with time and can be modified through social and cultural influences, human perceptions that involve memories, emotions and the senses (Church *et al.*, 2014; Jones *et al.*, 2016).

Previous reviews of ecosystem services associated with bivalve aquaculture (Coen *et al.*, 2007; Economics, 2009; Rose *et al.*, 2014), focused on oysters (Herbert *et al.*, 2012) and mussels (Lindahl *et al.*, 2005), with few data published on other major commercially important species, such as scallops, Japanese carpet shell and clams. There are strong geographical biases in the literature to date, with many studies from North America (Coen and Luckenbach, 2000; Grabowski and Peterson, 2007) and the Baltic (Petersen *et al.*, 2016; Timmermann *et al.*, 2019), but relatively few from other parts of the globe such as other parts of Europe, South America and Asia. Until recently, with a few exceptions (Beseres Pollack *et al.*, 2013; Northern

Economics, 2009), there was a distinct lack of attempt made to quantify the services and their economic value, in part due to knowledge gaps. Much of the information on bivalve regulating services is based on oysters in the USA and mussels in the Baltic, and their ability to remove nitrogen and phosphorus, but few apply valuations to this (Molinos-Senante et al., 2011; Newell et al., 2005). The USA is also the only country with published estimates of their role in coastal protection (Borsje et al., 2011; Piazza et al., 2005). There is little data from other regions in the world and for other species and it is uncertain whether nitrogen and phosphorus removal rates differ regionally/globally. There is one study in the UK (Herbert et al., 2012) but this lacks in-depth analysis on regulating services. More importantly, whilst some data on regulating services from Asia was found (Zhou et al., 2002), there is relatively little data considering they are the largest producers of bivalves in the world. This is addressed in chapter 2, where the ecosystem services in bivalve aquaculture are collated, focussing on species which are commercially harvested (e.g. mussels, clams, scallops and oysters). For the first time, this thesis puts value at the global scale, of the ecosystem services provided by bivalve aquaculture. While knowledge gaps hinder a comprehensive valuation, by using the values collated through the literature it is possible to make a partial estimate of the value of ecosystem services, including values for nutrient remediation and the use of oyster shell as aggregate.

Nutrient remediation remains one of the largest areas of interest for bivalve aquaculture with academics and policymakers. Bivalves are effective filter-feeders, removing particulate organic matter including phytoplankton from the water column (Newell *et al.*, 2005; Saurel *et al.*, 2014). In recent years mussel farms have been discussed as a mechanism of reducing the impact of terrestrial nutrient inputs to estuaries through their ability to filter phytoplankton and incorporate carbon (C), nitrogen (N) and phosphorus (P) into their shells and tissue (Clements and Comeau, 2019; Petersen *et al.*, 2019; Rose *et al.*, 2015). Paerl (2009) identify that to effectively deal with eutrophication it is important to remove both N and P. These are both taken up and used in both shell and tissue growth, and this is removed from the marine ecosystem when the animals are harvested (Carmichael *et al.*, 2012; Cerco and Noel, 2007).

A range of environmental factors may influence mussel biology and potentially vary the capacity for N and P retention in tissue and shell. Temperature is a key factor which has long been understood to influence the metabolism of the blue mussel *Mytilus edulis* (Widdows, 1973), including filtration rates, absorption and the utilisation of available food (Zippay & Helmuth, 2012). *M. edulis* are more likely to grow faster or larger at warmer sites (Lesser *et al.* 2010), whereas low salinity has been shown to reduce filtration and growth rates (Seed and

Suchanek, 1992). Cultivation methods have been shown to affect the growth rates of mussels, with faster growth in rope culture than bottom culture (Kamermans and Capelle, 2019). Food availability may also influence growth rates, and this is often represented by chlorophyll concentration (Rosland *et al.*, 2009; Thomas *et al.*, 2011). Suspended particulate material (SPM) has been used as a proxy for food supply (Smaal and Haas, 1997), whilst the tidal range has been used as a proxy for tidal velocity and hence water flow and food supply (Coen and Luckenbach, 2000). The amount of nutrient removal in harvested shellfish will vary based on tissue and shell nutrient retention, which in turn is influenced by environmental factors such as food supply, temperature and seasonal spawning cycles (Hawkins and Bayne, 1985; Rodhouse et al., 1984; Rose et al., 2014; Smaal and Vonck, 1997). Additionally, the composition of the shells of bivalves have been shown to vary during the process of biomineralisation of the shell (Richardson et al., 2015). During this process many elements are incorporated, together with the calcium that forms the bulk of the skeletal calcium carbonate structure of the animal, at the time of calcification (Piwoni-Piórewicz et al., 2017).

Therefore, as these factors could potentially influence the amount of C, N, and P stored in the mussels, in **chapter 3** of this thesis, a spatial survey around the UK is carried out. This spatial survey focuses on mussels (*M. edulis*) as they are the most common aquaculture produced species in the UK (Ellis *et al.*, 2015) and assesses regional variation in C, N and P content in tissue and shells as well as the potential relationships with a range of environmental predictors such as estuarine nutrient loading, salinity, temperature and culture method. This is upscaled with the weight of mussels collected, to calculate the kg C, N, and P content per tonne of live mussels.

Significant seasonal changes in meat yield has been observed in cultivated mussels and of mussels obtained from natural beds due to gonad development and spawning (Grkovic et al., 2019). The proximate composition of protein, carbohydrate, and lipids has also been found to show seasonal change (Dare and Edwards, 1975; De Zwaan and Zandee, 1972). The most noticeable change in composition was increased glycogen content in mussels harvested during late summer and fall, and this increase was attributed to the type of food which the blue mussels ingested (Slabyj et al., 1978). Studies have shown the typical seasonal pattern observed in mussel tissues is a result of spawning period in spring and summer characterised by weight loss; then a period of glycogen storage; followed by a period of gonad development in late autumn and winter (Gabbott, 1983). However, it has been highlighted that there is a lack of information on seasonal variation of nutrient content within sites (Rose *et al.*, 2014).

There is debate within the literature that C stored in shell represents a long-term sink. Calcifying organisms are directly involved in two processes that release CO_2 . First, CO_2 is released via the catabolism of ingested organic matter:

 $CH_2O + O_2 \rightarrow CO_2 + H_2O$

and, second, it is released via calcium carbonate (CaCO₃) formation by biogenic calcification:

 $Ca^{2+} + 2HCO_3^{-} \leftrightarrow CaCO_3 + CO_2 + H_2O$

This release of CO₂ also induces shifts in the carbonate system:

 $CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO^-_3 \leftrightarrow 2H^+ + CO^{2-}_3$

The balance between the CO_2 released in respiration and biogenic calcification and the net C sequestered as calcium carbonate, as shown above, have been used to evaluate the role of bivalves in the CO_2 cycle (Filgueira et al., 2019).

The deposition of calcium carbonate generates a small net sequestration explicitly resulting from individual biocalcification given that the precipitation of 1 mol of CaCO₃ releases approximately 0.6 mol of CO₂ (Ware et al., 1992). But this net sequestration (1.0 - 0.6 = 0.4)mol of CO_2 per mol of $CaCO_3$) is not enough to compensate the CO_2 that is released due to the catabolism of organic matter. Controversially, Tang et al. (2011) proposed that bivalve (and seaweed) aquaculture could increase atmospheric CO₂ absorption within coastal ecosystems. This paper did not account for the release of CO₂ via respiration in their budget, but argued for the inclusion of some relevant ecosystem effects when scaling up from the individual to the ecosystem level. For example, Tang et al. (2011) suggested that in a strongly autotrophic system, CO₂ released by carbonate precipitation may be used by photosynthetic organisms, resulting in a lower transfer of CO₂ from water to the atmosphere. They also suggested that removing shells from the oceans presents a long-term carbon sink, although this would then remove the buffering capacity of respiratory acids to the environment (Waldbusser et al., 2013). These effects on water chemistry highlight that a simple multiplicative extrapolation from the individual to the ecosystem level oversimplifies the role of bivalves in the ecosystem and the sequestration of CO₂ in the shell is not enough to compensate the release generated during the respiration of organic matter (Filgueira et al., 2019). When valuing ecosystem services, it has been recognized that humans harvest bivalves

to provide food and consequently shells should be considered waste. Filgueira et al. (2019), therefore, raise the argument that a different CO_2 budget should be calculated for product (tissue) and waste (shell). Going on to suggest that under these considerations, bivalve shells can be considered net sinks of CO_2 and consequently provide additional ecosystem services besides the food provided by the tissue. Therefore, the UK spatial survey (**Chapter 3**), identified the amount of C in tissue and shell that was removed, but it could not suggest if this C was sequestered, due to a comprehensive lack of data.

Comparatively, it was possible to draw conclusions of the amount of N and P that are removed from the system. If mussels are to be used as a tool for the removal of nutrients from the marine environment (Petersen *et al.*, 2019, 2016; Timmermann *et al.*, 2019), it is important that they are harvested at a time when the nutrient contents are high. Therefore, chapter 4 presents a temporal study looking at seasonal differences in C, N, and P percentage content and test for differences in two nearby but contrasting sites. It presents the annual trends between January 2018 and January 2019. This chapter upscales C, N, and P percentage content with the weight of mussels collected, to calculate the kg C, N, and P content per tonne of live mussels.

The global assessment carried out by van der Schatte Olivier *et al.* (2018, chapter 2) estimated roughly that global, non-food bivalve aquaculture services could be worth \$6.47 billion (\$2.95 billion–9.99 billion) per annum. One of the main issues raised in that study, and subsequently in other reports (Mcleod and Mcleod, 2019) are knowledge gaps. The services quantified in the global study were nutrient (nitrogen and phosphorus) removal, and the use of oyster-shell waste as aggregate. Services unable to be quantified or valued included: nursery grounds, bivalve use as fertilisers, pearls and nacre, biological accumulation of E. coli and other pathogens, shoreline defence, wildlife watching, use in education and research and the value of seafood festivals. The global valuation required broad assumptions, utilising what literature was available, with a lack of high-resolution data. With this information, in chapter 5, the data collected throughout the thesis is collated in combination with the tonnages of mussels produced in the UK. Then using UK specific values for C, N, and P, it is combined with economic valuations for nutrient removal and for using shell as an aggregate, provides the first country specific quantification and valuation of ecosystem services.

The UK mussel aquaculture industry has decreased in size between 2012 to 2018 (Eurostat (https://ec.europa.eu/eurostat/data/database)

and FAO (http://www.fao.org/fishery/statistics/software/fishstatj/en)). This is largely due to decreases in wild spat fall, which has even led to the establishment of a pilot-scale blue mussel hatchery in the Shetland Islands in order to ensure the provision of spat for rope aquaculture, allowing the Scottish industry to reduce its reliance on wild resources (Adamson et al., 2017). Mussel growers in the south of the UK generally experience high rates of wild mussel settlement, therefore, by installing spat collectors in the water column in these areas, mussel larvae will naturally attach themselves, with no extra costs apart from providing a substrate such as ropes (Suplicy, 2018; van den Burg et al., 2017). This could be a source for restocking mussel beds to production levels of previous years. Another problem faced by the mussel industry since 2016, has been additional concerns following the announcement of the exit of the UK from the European Union, which accounts for around 80% of mussel exports (Symes and Phillipson, 2019). This is despite the Welsh government (2013) and Scottish government (Scotland Food & Drink, 2016) stating they want to double the economic income of the aquaculture industry. Therefore, in chapter five, four scenarios are used to quantify and contrast these potential impacts of anthropocentric or environmental drivers of change on the associated ecosystem services.

The global review of ecosystem services of bivalve aquaculture (Chapter 2, van der Schatte Olivier *et al.*, 2018) provided the template for an additional paper on the ecosystem services of cockles, which I contributed to (Carrs *et al.*, 2020). The paper focused on the common cockle (Cerastoderma edule), a non-cultured bivalve species. In a similar manner to bivalve aquaculture, this paper identified that 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.

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1.2 Thesis structure

The structure of the thesis is split into six chapters. **Chapter 1** is a general overview, then chapters two to five are each written as a stand-alone paper. The main thesis then ends with **chapter 6** which is a general discussion, addressing the points raised in the general introduction. During the writing of this thesis, I contributed to another paper on ecosystem services "Ecosystem services provided by a non-cultured shellfish species: the common cockle *Cerastoderma edule*", which is included as an appendix.

Chapter 1: General introduction

Chapter 2 identifies the ecosystem services provided by global bivalve aquaculture and attempt to put a valuation on as many as possible at a global scale using the literature and FAO figures on bivalve aquaculture production.

Chapter 3 investigates regional variation in C, N and P content in tissue and shells of *M*. *edulis* in estuaries around the UK, and relationships with a range of potential environmental predictors such as estuarine nutrient loading, salinity, temperature and culture method.

Chapter 4 investigates seasonal differences in C, N, and P percentage content and tests for differences in two nearby but contrasting sites. It incorporates the weight of mussels collected to upscale and calculate the kg C, N, and P content per tonne of live mussels.

Chapter 5 uses results from the spatial data collected around the UK to calculate the effect on ecosystem services and resulting economic value under four scenarios for the UK mussel industry. (Scenario 1 – Status quo, Scenario 2 – Trade failure, Scenario 3 – Recovery, and Scenario 4 – Expansion).

Chapter 6: General discussion

Appendix: "Ecosystem services provided by a non-cultured shellfish species: the common cockle *Cerastoderma edule*", collates 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. Within this, I wrote the sections on provisioning services, including shell by-products, such as poultry grit and for construction, carried out a European valuation for the ecosystem services of cockle fisheries, and I contributed parts of the methodology.

2 A global review of the ecosystem services provided by bivalve aquaculture

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This paper was first published in Reviews in Aquaculture on the 12th of November 2018. Available from: <u>https://onlinelibrary.wiley.com/doi/full/10.1111/raq.12301</u>. The PhD candidate was the first author and with supervision, wrote and calculated all values within the study.

2.1 Abstract

Bivalve shellfish aquaculture provides many benefits to society, beyond their traditional market value. This study collates the evidence available on the provisioning, regulating and cultural ecosystem services provided by the bivalve species commonly used in aquaculture. For the first time, it synthesises this evidence to provide a global assessment of the potential market and non-market economic value of bivalve aquaculture. Bivalves are filter feeders, filtering water and particulates, creating substrates which provide habitat to act as nursery grounds for other species. Goods from provisioning services include meat, worth an estimated \$23.9 billion as well as, pearls, shell and poultry grit, with oyster shell being the most important, with a global potential worth of \$5.2 billion. The most important regulating services are nutrient remediation. Cultivated bivalves remove 49,000 tonnes of nitrogen and 6,000 tonnes of phosphorus, worth a potential \$1.20 billion. Currently, there is little evidence on the cultural services per year of bivalve aquaculture, but these cultural values are broad ranging, although difficult to quantify. Our assessment indicates that the global, non-food bivalve aquaculture services are worth \$6.47 billion (\$2.95 billion–9.99 billion) per annum. However, this is likely to be an underestimate of the true value of bivalve aquaculture as there are significant gaps in evidence of the value for a number of key services. The analysis presented here can be used to indicate the likely scale of payments for ecosystem services provided by bivalve aquaculture, prior to more detailed assessments.

Keywords: bivalves, blue carbon sequestration, cultural services, nutrient removal, regulating services, valuation.

2.2 Introduction

There has been consistent growth in aquaculture production in recent decades, which in 2016 represented 41% of global fisheries and aquaculture food production (SAPEA 2017). Lower trophic species, including shellfish and algae, currently make up about half of all aquaculture production and offer potential for significant contribution to sustainable growth in the global aquatic food supply (Science Advice for Policy by European Academies 2017). Bivalves (primarily clams, mussels and oysters) accounted for 16 million tonnes of coastal and marine animal aquaculture in 2015, with an estimated market value of \$17.1 billion (FAO 2016).

In addition to food supply (provisioning services), there is a growing recognition of the wider ecosystem benefits of bivalve aquaculture in coastal waters, including regulating services such as carbon sequestration, nutrient remediation, coastal defence and indirect benefits arising from shellfish beds and reefs (Shumway *et al.* 2003; Lindahl *et al.* 2005; Rönnbäck et al., 2007; Northern Economics 2009; Herbert *et al.* 2012; Seitz *et al.* 2014). However, there remain substantial gaps in the published literature on non-market benefits, and some services remain largely unquantified. For example, the majority of studies focus on only a few regulating services such as carbon sequestration (Filgueira *et al.* 2015) or nutrient remediation (Newell *et al.* 2005). Quantifying cultural services is an acknowledged challenge in many domains (Chan *et al.* 2012) and the cultural services of bivalve aquaculture have not been assessed in any capacity. Meanwhile, the literature on provisioning services is dominated by a focus on constraints to production and the possibilities for expansion (Gentry *et al.* 2017).

Previous reviews of ecosystem services associated with bivalve aquaculture (Newell 2004; Coen *et al.* 2007; Northern Economics 2009; Herbert *et al.* 2012; Rose *et al.* 2014), have focused on oysters (Herbert *et al.* 2012) and mussels (Lindahl *et al.* 2005), with few data published on other major commercially important species, such as clams (Nizzoli *et al.* 2006). There are also strong geographical biases in the literature to date, with many studies from North America and the Baltic, but relatively few from other parts of the globe such as other parts of Europe, South America and Asia. Furthermore, with a few exceptions (e.g. Northern Economics 2009; Beseres Pollack *et al.* 2013), there is a distinct lack of quantification of the services and their economic value.

Coupled with growing interest in the ecosystem services provided by aquaculture, there is an increasing policy focus on this area. For example, in Europe, under the EU's biodiversity

strategy member states had an obligation to map and assess the state of ecosystems and their services in their national territory by 2014, assess the economic value of such services, and promote the integration of these values into accounting and reporting systems at EU and national level by 2020 (Bourguignon 2015).

In this paper, the value the ecosystem services provided by bivalve aquaculture are quantified, focussing on species which are commercially harvested (e.g. mussels and oysters). Utilising the Common International Classification of Ecosystem Services (CICES) typology (European Environment Agency 2012), which provides a hierarchical system, building on the Millennium Ecosystem Assessment (MEA) and The Economics of Ecosystem and Biodiversity (TEEB) classifications but tailored to accounting (Bateman *et al.* 2011; Boerema *et al.* 2016), allowing us to look at the economic value where possible. Although, CICES does not classify supporting services, this study provides evidence on these supporting services as these underpin the delivery of the final services, to which an economic value can be assigned (Bateman *et al.* 2011).

The structure of the paper is as follows. Firstly, it describes the supporting services provided by bivalve aquaculture. It then synthesises the evidence that quantifies and values the three categories of final ecosystem services (Provisioning, Regulation and Maintenance and Cultural). In each section, it briefly introduces the services, referring to the processes and mechanisms that underpin them. This is followed by a review of quantitative evidence of both the scale of ecosystem services and key underlying mechanisms. Next, it uses these data to conduct a global assessment of the potential value of ecosystem services from bivalves. Finally, discussing challenges raised in this assessment, and provide an overview of knowledge gaps.

2.3 Methods

The analysis is based on keyword searches of literature databases using Google Scholar and Web of Knowledge. Keywords for searches were based on terms often used in bivalve aquaculture, including searches for species names (e.g. mussel, Mytilus, oyster, Crassostrea, etc.) and services and functions (e.g. provisioning, regulating, cultural, filtration, carbon, nutrient remediation, carbon trading, coastal defence, etc.) on publications between 1918 and 2018. Including grey literature using web searches and databases available on websites of trade bodies, non-governmental and conservation organisations. From the studies identified through literature searches, those where bivalve aquaculture and/or restoration projects had quantified

activities, processes or functions which fell within the CICES sections of Provisioning, Regulation and Maintenance and Cultural services were selected.

To allow comparison between studies, units were converted to a standardised format where possible. For pumping rates of bivalves, the units were converted into litre h^{-1} . Bivalve production was converted to tonnes. Nitrogen or phosphorus removal were respectively converted to t N ha⁻¹ yr⁻¹ or t P ha⁻¹ yr⁻¹ and the denitrification rates converted to μ mol N m⁻² h^{-1} , or to kg N t⁻¹ shellfish. Where it was not possible to convert the units, they were presented as kg N t⁻¹ or as % of N load d⁻¹. Rates of carbon sequestration were converted to t C ha⁻¹ yr⁻¹.

All economic values are expressed as US dollars (2017 values). Economic values were adjusted to account for inflation to 2017 and then where necessary converted to USD using purchasing power parities (PPPs) (Hamadeh *et al.* 2017).

To carry out a global upscaling of the potential value of the ecosystem services, we used FAO figures of global aquaculture production (http://www.fao.org/fishery/statistics/global-aquaculture-production/query/en). Species tonnages included those for mussels, oysters, clams, cockles, arkshells, scallops and pectens. We then used meat yields (the ratio of meat to whole weight including shell (Science, 2015)) to approximate the wet tissue weight (Error! Reference source not found. Table 1). Shell weight was calculated using condition indices to convert from the total production weights, accounting for wet tissue weight to allow for water (liquor) retained by live bivalves. We used the condition indices (CI = wet meat weight/ (Live weight- shell weight) x 100) ((WMW/(LW-SW)) x 100) reported in both Okumuş & Stirling (1998) and Muniz *et al.* (1986) to calculate the shell weight for mussels and oysters. For clams we used the condition index (CI = (Meat dry weight/Shell dry weight) x 1000) ((MDW/SDW) x 1000) reported in Orban *et al.* (2006) to calculate shell weight. Scallops gape when harvested and therefore the landed weight does not include liquor, so it was possible to simply remove the meat weight from total weight using Ricciardi & Bourget (1998) conversion factors.

The C, N and P composition percentages of meat and shell were calculated using values from the literatures for each species (Çelik *et al.*, 2012; Hardy and Smith, 2001; Science, 2015; Stroud, 1981). Where data for a species were not available an average of all bivalve species was applied. Carbon content was calculated for shell only, as carbon in meat was considered as non-sequestered. To estimate economic values for nutrient removal, the alternative cost of nitrogen removal (\$8,830 tonne⁻¹ (Beseres Pollack *et al.*, 2013)) and the shadow price (the

estimated price of a good or service for which no market price exists) for phosphorus removal (395,495 tonne⁻¹ (Molinos-Senante *et al.*, 2011)) were applied. Due to a lack of consensus on whether calcification represents a source or a sink of CO₂, the potential value of carbon sequestration was not used in the final valuation. To calculate the potential value of oyster shell, the values found for shell aggregate (Morris *et al.*, 2018) were used and these were applied to the tonnage of waste oyster shell (**Error! Reference source not found.** Table 1).

Table 1 Values extracted from peer reviewed sources used to carry out global upscaling calculation and analysis. Mean values are presented with the range of values included in brackets.

Clam Meat yi	eld		18.5% (18-19%)			(Science, 2015)
Mussel Meat			22.06% (17.43-26.69%)			(Çelik et al., 2012)
Oyster Meat y			10.75% (6-18%)			(Çenk et al., 2012) (Stroud, 1981)
Scallop Meat			13% (11-15%)			(Hardy and Smith, 2001)
	5					(,,,,
Condition ind	lex clam ((MI	DW/SDW)	66.1			(Orban et al., 2006b)
x 1000)						
Condition	index	Mussel	45.9			(Okumuş and Stirling,
((WMW/(LW	-SW)) x 100)					1998)
Condition	index	Oyster	72.3			(Muniz et al., 1986)
((WMW/(LW	-SW)) x 100)					
			C (% of dry weight)	N(% of dry weight)	P (% of dry weight)	
Clam (Shell/T	ïssue)		C (% of dry weight)	-		
Clam (Shell/T Mussel (Shell/				weight)	weight)	
	/Tissue)		11.41/43.70	weight)	weight) 0.04/0.79	
Mussel (Shell/	/Tissue) Tissue)		11.41/43.70 12.68/45.98	weight) 0.25/10.28 0.84/9.08	weight) 0.04/0.79 0.05/0.92	
Mussel (Shell/ Oyster (Shell/ Scallop (Shell	/Tissue) Tissue)	ry weight	11.41/43.70 12.68/45.98 11.85/44.81	weight) 0.25/10.28 0.84/9.08 0.16/7.85	weight) 0.04/0.79 0.05/0.92 0.04/0.91	(Ricciardi and Bourget,
Mussel (Shell/ Oyster (Shell/ Scallop (Shell	/Tissue) Tissue) /Tissue)	ry weight	11.41/43.70 12.68/45.98 11.85/44.81 11.72/44.86	weight) 0.25/10.28 0.84/9.08 0.16/7.85	weight) 0.04/0.79 0.05/0.92 0.04/0.91	(Ricciardi and Bourget, 1998)
Mussel (Shell/ Oyster (Shell/ Scallop (Shell Shell free we conversion	/Tissue) Tissue) /Tissue)	• 0	11.41/43.70 12.68/45.98 11.85/44.81 11.72/44.86	weight) 0.25/10.28 0.84/9.08 0.16/7.85	weight) 0.04/0.79 0.05/0.92 0.04/0.91	C ·
Mussel (Shell/ Oyster (Shell/ Scallop (Shell Shell free we conversion	/Tissue) Tissue) /Tissue) t weight to d	• 0	11.41/43.70 12.68/45.98 11.85/44.81 11.72/44.86	weight) 0.25/10.28 0.84/9.08 0.16/7.85	weight) 0.04/0.79 0.05/0.92 0.04/0.91	C ·

2.4 Supporting services

Supporting services underpin the delivery of all other ecosystem services, Supporting services provided by shellfish include: the cycling of nutrients through filter feeding and the creation of sediment (Cranford *et al.* 2007); increasing seabed roughness; and providing habitats for other organisms (Seitz *et al.* 2014; Turner & Schaafsma 2015).

2.4.1 Increasing seabed roughness

Shellfish beds impact upon water flows at different scales: (1) at a micro scale (mm to cm) via biomixing created by the jet of water from the exhalant siphons and by increasing bed roughness via the mussel shell shape; and (2) at a macro scale (tens of metres), via the topographic variation of the mussel bed, e.g. alternation between mussel patches and bare patches of sediment (Butman *et al.* 1994; Saurel *et al.* 2013; Folmer *et al.* 2014). This mixing of water underpins several supporting or intermediate services including nutrient cycling, alternation of turbidity, and the accretion of sediments and moderating wave energy.

2.4.2 Providing habitat for other organisms

Both mussels and oysters can naturally form reefs, which perform a wide range of ecological functions. They provide refuge between the shells (Snover & Commito 1998) and a hard substrate for other species of invertebrates and algae to settle (Brumbaugh *et al.* 2006). Studies have shown that species diversity can be greater on Pacific oyster reefs than within the habitat on which the oysters settle (Herbert *et al.* 2012) and act to facilitate biodiversity and re-establish benthic communities on shores where Ostrea edulis has become extinct (Zwerschke *et al.* 2018). The artificial structures used in bivalve aquaculture also provide a habitat for organisms to adhere to, with racks, cages, nets, ropes and the shells themselves all providing a suitable substrate for colonisation (Shumway *et al.* 2003). This can lead to richer ecological communities, supporting numerous trophic levels not only at the reefs themselves, but in the surrounding area (Ragnarsson & Raffaelli 1999; Brumbaugh *et al.* 2006; Koivisto & Westerbom 2010). In the northern Baltic Sea, mussel beds support a range of suspension

feeders such as barnacles, polychaetes and ascidians. The mussels themselves are often encrusted in barnacles. The mussels are predated on by crabs and starfish and several species of wading birds (Mainwaring *et al.* 2014). Intertidal mussel beds support a high taxonomic diversity and abundance of benthic organisms and are important foraging grounds for many avian species (Waser *et al.* 2016). The reef itself forms accumulations of 'mussel mud', composed of faeces, pseudofaeces and sediment, which also supports a diverse range of infauna (Mainwaring *et al.* 2014). In the northern Baltic, mussel mud increased the abundance of softbottom species such as polychaetes and nemerteans (Bick & Zettler 1994; Koivisto & Westerbom 2010).

2.4.3 Indirect economic benefits to other services/habitats

Structured habitats provided by bivalves can lead to measurable increases in production of finfish and invertebrates that are important for commercial and recreational fisheries (Coen *et al.*, 2007), with an economic benefit (Northern Economics 2009). Peterson *et al.* (2003) used both demographic and growth models to estimate that in the southeast United States, oyster reef restoration yielded an additional 2,600kg ha⁻¹ yr⁻¹ of fish and large mobile crustacean produce. Grabowski and Peterson (2007) then showed that the long term commercial value of the fish and crab species in the same area was greater than the value of oyster production (Grabowski and Peterson, 2007), and using commercial landing values of each species demonstrated that the added value from oyster reefs equated to \$3,811 ha⁻¹ yr⁻¹. The increase in fish numbers also benefits recreational fishers; Isaacs *et al.* (2004) estimated the value of recreational fishing over oyster reefs in Louisiana using contingent valuation and found the average net willingness to pay among resident saltwater recreational fishers was \$13.61 giving a median value of \$3 million for sports fishing provided by oyster beds in Louisiana .

2.5 **Provisioning services**

Provisioning services include all material and energy outputs from an ecosystem that may be exchanged or traded, as well as consumed or used directly in manufacturing (European Environment Agency 2012). Within bivalve aquaculture provisioning services are split between two divisions: the provision of nutrition (food), and provision of materials such as fertiliser, construction, grit for poultry and in jewellery (Table 2).

Division	Group	Class	Examples and indicative benefits
Nutrition	Biomass	Wild animals and their outputs	Food production e.g Shellfish meat
			caught from commercial, recreational
			and subsistence fisheries
		Reared animals and their outputs	Food production e.g Shellfish meat
			produced through aquaculture
			production
Materials	Biomass	Materials from plants, algae and	Crushed shells used in the poultry
		animals for agricultural use	industry
			Using the ground flesh or associated
			nutrient rich mud's as sources of
			fertiliser. Crushed shell as a source of
			lime
		Fibres and other materials from plants,	Shells used as construction materials
		algae and animals for direct use or	(aggregate and lime)
		processing	Pearls/mother of pearl

Table 2 Provisioning services of shellfish aquaculture using the CICES system for classification

2.5.1 Food production (nutrition, biomass, reared animals)

The value of bivalve aquaculture has most frequently been calculated as the market value of the meat that is produced. The value fluctuates as aquaculture production increase and decrease, and as market demands change. The total aquaculture production of bivalves for human consumption in 2015, was 14.65 million tonnes (Table 3), with an estimated market value of \$23.92 billion (http://www.fao. org/fishery/statistics/global-aquaculture-production/query/ en). (FAO 2016) Asia is the largest regional global producer, dominated by China, with 12.4 million tonnes of bivalves produced in 2015. On a much smaller scale of production, Europe is the next largest producer, with only 0.6 million tonnes and then the Americas with 0.46 million tonnes.

Table 3 Annual aquaculture production by continent, showing top three countries and dominant aquaculture species in 2015. Values adjusted for inflation to 2017. FAO [online] [Accessed 26 June 2017].

Region	Country	Predominant species farmed	National total for all	Value (\$ 000)
			Species (Tonnes)	
Africa		Mussels, Oysters	8,703	8,703
	South Africa	Mytilus galloprovincialis	3,987	3,987
	Namibia	Crassostrea gigas	1,850	1,850
	Senegal	Crassostrea gigas	1,798	1,851
Americas		Mussels, Oysters, Clams,	463,419	2,300,788
		Cockles, Arkshells, Scallops,		
		Pectens		
	Chile	Mytilus chilensis	214,531	1,783,157
	United States	Crassostrea virginica	159,175	257,083
	of America			
	Canada	Mytilus edulis	36,311	69,852
Asia		Mussels, Oysters, Clams,	13,479,192	19,983,869
		Cockles, Arkshells, Scallops,		
		Pectens		
	China	Crassostrea spp	12,389,502	18,459,094
	Japan	Patinopecten yessoensis	413,028	825,029
	Taiwan	Crassostrea gigas	323,926	309,876
Europe		Mussels, Oysters, Clams,	608,957	1,106,374
		Cockles, Arkshells, Scallops,		
		Pectens		
	Spain	Mytilus galloprovincialis	227,805	144,860
	France	Crassostrea gigas	124,481	513,317
	Italy	Mytilus galloprovincialis	100,345	173,728
Oceania		Mussels, Oysters, Clams,	95,054	605,693
		Cockles, Arkshells, Scallops,		
		Pectens		
	New Zealand		78,720	507,576
		Perna canaliculus		
	Australia	Crassostrea gigas	16,320	77,601
	Cook Islands	Tridacna spp	5	16
World			14,649,532	23,919,193

2.5.2 Usage of shell (materials, biomass, agricultural uses)

While the tissue is consumed and respired, the shell is usually discarded and these shells act as a long-term carbon store (Mangerud and Gulliksen, 1975). Currently waste disposal of shell costs up to \$290 tonne-1 in Australia (Yan and Chen, 2015), however, using shell as a product could provide income instead of a cost. One potential trade-off is that destructive uses of shell such as for poultry grit or agricultural lime will prevent their use as a carbon store, so not all of the non-food services are compatible. For this reason, the analysis only valued the use of shell in aggregate but not poultry grit.

2.5.3 Poultry grit (materials, biomass, agricultural uses)

Global poultry production is estimated to be approximately 21 billion birds per year, producing 1.1 trillion eggs and approximately 90 million tonnes of meat annually (Blake & Tomley 2014). Bivalve shells are used in some poultry grit (ground-up shell is mixed with ground granite and fed to poultry to help digestion and to provide calcium for egg shells). The main species used are oyster and cockle shells because their shells do not break down into sharp shards: unlike mussel and scallop shells. Little information is available on the contribution of shell to poultry grit. Values for oyster shell sold as poultry grit range between \$320 and \$2,400 per tonne (Morris *et al.* 2018).

2.5.4 Fertiliser and lime (materials, biomass, agricultural uses)

Agricultural crops require macro-nutrients such as nitrogen, phosphorus and potassium, of which nitrogen is the most important, as it has the largest effect on crop yield and quality (Campbell 1996). Other important nutrients include magnesium (Bot & Benites 2005) and, due to improvements in air quality, in some regions it has become necessary to add sulphur-containing fertilisers to replace sulphur previously provided by air pollution (ADAS UK Ltd 2006; Jones *et al.* 2014).

Shellfish waste material (shell and unused tissue), is nutrient rich, containing many of the macro- and micro-nutrients required for agriculture. ADAS (2006) compared nutrient contents of shellfish waste with other organic manures which have been used in agriculture (Appendix A – Table A 3). The ratio of nitrogen, phosphate and potash in the shellfish-based compost is approximately 2:1:1, which closely matches the Agricultural improvement of acid soils involves application of lime or other calcareous materials (Yao *et al.*, 2014). Crushed oyster shell can be used as a soil conditioner, stimulating the growth of soil and rhizospheric microorganisms. Addition of 0.3 t ha⁻¹ doubled the number of bacteria, actinomyces and

nitrogen-fixing bacteria (Guoliang *et al.*, 2003). In Korea, oyster-shell meal, was tested as a soil liming material (Lee *et al.* 2008) and significantly increased soil pH and soil nutrients such as soil organic matter, available phosphorus, and exchangeable cations in silt loam and sandy loam soils, when applied at rates of up to 16 t ha⁻¹ although this is currently not a common practice.

2.5.5 Shucked shells used as construction materials (materials, biomass, construction uses)

Oyster shell is used as a construction material in sea defences in North America. This is because the shells become tightly packed and are more lightweight than traditional shoreline protection materials (Borsje et al., 2011; Piazza et al., 2005). Oyster shells have been used throughout history for construction of buildings, most commonly in their burnt form as lime, also known as quicklime (calcium oxide) (Sheehan and Sickels-Taves, 2002). More recently there has been growing research into the use of crushed shells in place of sand, aggregate and cement (Kumar et al., 2016; Ohimain et al., 2009). Environmentally friendly methods of aggregate extraction and material selection are in demand, because over-extraction of natural aggregate can lead to the destruction of ecosystems associated with marine sediments (Yoon et al., 2004). Kumar et al., (2016) found that replacing 10% of standard aggregate in concrete with shell and lime created a product with the same strength, however at 20-30% replacement this led to gradually decreasing strength. Two billion tons of aggregate are produced each year in the United States and production is expected to increase to more than 2.5 billion tons per by the year 2020 (Kumar et al., 2016). In terms of economic value, shell aggregate can cost between \$240 to \$2,400 tonne⁻¹, depending on whether the shells are whole or crushed. There is a growing trend to use bivalves within (Morris et al., 2018) therefore providing a potential use for waste products of the aquaculture industry.

2.5.6 Pearls and mother of pearl (materials, biomass, fibres and other materials from animals)

Pearls have long been valued for their lustre, and made into earrings, necklaces, pendants, bracelets, rings and other jewellery. Pearl production in 2009, yielded around 40 tons of pearls (Carino & Monteforte 2009). Another product ~ derived from bivalves is mother of pearl or nacre, this is a naturally occurring layer that lines some mollusc shells. Throughout history has been used to make pearl buttons and jewellery. It was also commonly inlaid into boxes and other furniture, particularly in China (Southgate & Lucas 2008). No figures on the quantity traded or its value could be found. The pearl industry has declined in recent years, with

production in 2009 being half of what it was in 1993. From an estimated \$912 million in 1993, the wholesale value of pearls dropped to approximately \$570 million in 1999; and for 2009, the value was estimated to be approximately \$422 million, although there was no current valuations for the industry. This decrease has been attributed to competition between producers, increasing cost of production and to a lesser degree marine pollution affecting the health of the oyster populations used (Muller \in 2013).

2.6 Regulating services

Regulating services are the ways in which ecosystems control or modify biotic or abiotic parameters that define the environment of people. These are ecosystem outputs that are not consumed but affect the performance of individuals, communities, and populations as well as their activities (European Environment Agency 2012). A wide variety of specific regulating services are performed by bivalve beds, which include biochemical accumulation, biological accumulation, carbon sequestration, nutrient removal and coastal defence (Table 4).

Division	Group	Class	Examples and indicative benefits
Regulation of	Mediation of	Bio-remediation by	Cycling of nutrients, creation of sediment,
biophysical	waste, toxics	micro-organisms,	biochemical accumulation of nitrogen and
environment	and other	algae, plants, and	phosphorus, and deposition into sediments
	nuisances	animals	Biological accumulation e.g. E. coli into shellfish,
			Pathogen deposition into sediments
		Filtration/sequestratio	Carbon sequestration in the form of calcium
		n/storage/accumulatio	carbonate in shells, removing CO ₂ from the system,
		n by micro-	Carbon deposition
		organisms, algae,	
		plants, and animals	
Mediation of flows	Liquid flows	Hydrological cycle	Increased seabed roughness, introducing turbulence
		and water flow	and reducing erosive potential of laminar flow of
		maintenance	water; increased food transport
	Mass flows	Mass stabilisation and	Reduced rates of shoreline and bed erosion
		control of erosion	Regulation of transport and storage of sediment
		rates	

 Table 4 Regulating services of shellfish aquaculture using the CICES system for classification

2.6.1 Cycling of nutrients, creation of sediment, biochemical accumulation of nitrogen and phosphorus and deposition into sediments (regulation of biophysical environment, mediation of waste, biochemical accumulation)

Bivalves are filter-feeding organisms, and are able to modify biogeochemical cycles by filtering large quantities of organic matter from the water column (Kellog et al., 2013). Phytoplankton use dissolved inorganic nitrogen for their growth, and when they are filtered from the water column by bivalves, along with other organic matter, the nutrients they contain are partly incorporated within the bivalves and partly deposited onto the surface of the sediment as faeces or psuedofaeces. Nitrogen in these biodeposits can also be transformed into unreactive nitrogen gas through denitrification and diffuse out of the sediment and back to the atmosphere (Kellog et al., 2013; Newell et al., 2005). Individual bivalves can filter large volumes of water ((Dame, 2011; Jørgensen et al., 1990; Saurel et al., 2013) Appendix - Table A 1). The greatest pumping rates are carried out by oyster species (26 to 34 l hr⁻¹), with other species ranging from 0.12 to 2.07 l hr⁻¹. This filtration removes large quantities of chlorophyll a, ranging between 28-92% (Appendix - Table A 1, Table A 2). Grabowski et al. (2012), Koivisto & Westerbom (2010) and Saurel et al. (2014) are good examples where chlorophyll α filtration rates in models can calculate the nitrogen removal through consumption of phytoplankton and detritus. This makes it possible to calculate the quantity of biological material and therefore nutrients being transferred from the water column, into the benthos.

Eutrophication of the aquatic environment has become an issue around the world (Kellogg *et al.* 2014). It is caused by excess nutrients (primarily nitrogen and phosphorus) leading to hypoxia, fish kills, loss of habitats such as submerged aquatic vegetation, and/or toxic blooms of algae (Bricker *et al.*, 1999, 2008; Rose *et al.* 2014). Nitrogen is considered the primary limiting factor in phytoplankton growth in the coastal environment and therefore has been the focus in eutrophication management (Ryther & Dunstan 1971; Ryther *et al.* 1972; Rose *et al.* 2014). The restoration of bivalve beds in Chesapeake Bay was recommended to mitigate environmental changes associated with eutrophication (Newell 1988; Rose *et al.* 2014), using bivalves as 'ecosystem engineers' (Waldbusser *et al.* 2013). Nitrogen and phosphorus are taken up and used for both shell and tissue growth, and this is removed from the marine ecosystem when the animals are harvested (Cerco & Noel 2007; Carmichael *et al.* 2012). Table 5 summarises quantities of nitrogen and phosphorus in tissue and shell of a number of species, while Table 6 summarises shell size. Together these can be used to estimate rates of removal

of nutrients from the marine environment by harvesting bivalves. On average, the dry weight of bivalve tissue contains 44.9% carbon, 9.3% nitrogen and 0.9% phosphorus, while shell contains 11.7% carbon, 0.3% nitrogen and 0.04% phosphorus (Table 6). Bivalves harvested in different seasons may have different contents of nitrogen and phosphorus, and the magnitude of these seasonal effects are unknown (Rose *et al.* 2014).

Nutrient Removal	Location	Density (m ⁻²)	Summary of findings	Source
Crassostrea gigas	Various	-	Net N removal 0.02 – 0.14 t N ha ⁻¹ yr	⁻¹ Rose <i>et al.</i> , 2015
0.0			(Modelled)	,
Crassostrea gigas	Valdivia	100	Net N reduction via filtration of between	nSilva <i>et al.</i> 2011
	estuary,		$0.7 - 1.2 \text{ t N ha}^{-1} \text{ yr}^{-1}$ (Modelled)	
	Chile			
Crassostrea gigas	Hiroshima	Raft	Removed ~10% of N load.day ⁻¹	Songsangjinda et al
	Bay, Japan	culture		2000
Crassostrea virginica	Potomac	-	Net N removal 0.09 t N ha ⁻¹ yr ⁻¹ (Modelled)Rose et al., 2015
	River, USA			
Crassostrea virginica	Mission-	408	Net 0.01 t N ha ⁻¹ yr ⁻¹ removed by harvest	Beseres Pollack et al
	Aransas			2013
	estuary,			
	Texas, USA			
Crassostrea virginica	Cape Cod,	400	< 1% - 15% of the total annual nitroger	nCarmichael et al.
	Massachusett		load, to 25% of all daily nitrogen loads	2012
	S			
Crassostrea virginica	Chesapeake	286	Net N removal by harvest 0.17-0.33 t N	NHiggins <i>et al</i> . 2011
	Bay, USA		ha ⁻¹ yr ⁻¹	
			And 0.023-0.047 t P ha ⁻¹ yr ⁻¹	
Crassostrea virginica	Chesapeake	-	Reduced total N concentration 10%- 159	6Cerco & Noel 2007
	Bay, USA		(Modelled)	
Mytilus edulis	Carlingford	-	Net N removal 0.12 t N ha ⁻¹ yr ⁻¹ (Modelled	Rose et al., 2015
	Lough,			
	Ireland			
Mytilus edulis	Pertuis	-	Net N removal 0.11 t N ha ⁻¹ yr ⁻¹ (Modelled	Rose et al., 2015
	Breton,			
	France			

 Table 5 Comparison of bivalve bioremediation-related studies for different rates of nutrient removal from the water column

Mytilus edulis	Skagerrak	Longlines	Net N removal by harvest, burial	
	Strait,		biogeochemical processes 1.45-1.5 t N ha	L
	Sweden		yr ⁻¹ (Lab based study)	
Table 5 continued				
Mytilus edulis	Orust-Tjorn	100kg,	Removed 10kg N tonne ⁻¹ of mussel	Haamer 1996
	system,	Long lines		
	Sweden			
Mytilus	Piran,	-	Net N removal 0.06 t N ha ⁻¹ yr ⁻¹ (Modelled)	Rose et al., 2015
galloprovincialis	Slovenia			
Mytilus	Chioggia,	-	Net N removal 0.02 t N ha ⁻¹ yr ⁻¹ (Modelled)	Rose et al., 2015
galloprovincialis	Italy			
Ostrea plicatula	Huangdun	-	Net N removal 0.11 t N ha ⁻¹ yr ⁻¹ (Modelled)	Rose et al., 2015
	Bay, China			
Pinctada imbricata	Port	-	Removed 7.5 kg N tonne ⁻¹ oyster;	Gifford et al., 2005
	Stephens,			
	Australia			
Pinctada imbricata	Port	-	Removal of 19 kg N tonne ⁻¹ oysters	Gifford et al. 2004
	Stephens,			
	Australia			
Ruditapes	Samish Bay,	-	Net N removal 0.25 t N ha^{-1} yr ⁻¹	Rose et al., 2015
philippinarum	USA		(Modelled)	
Venerupis decussata	Ria Formosa,	-	Net N removal 0.06 t N ha^{-1} yr ⁻¹	Rose et al., 2015
	Portugal		(Modelled)	
Denitrification				
Crassostrea virginica	Bogue	-	Denitrification removal 0.02 t N ha ⁻¹ yr ⁻¹	Piehler & Smyth
	Sound, USA			2011
Crassostrea virginica	Chesapeake	-	Denitrification removes 5 x 10 ⁻⁴ kg N g	Newell et al. 2005
	Bay, USA		oyster (Modelled)	
Mytilus	Goro lagoon,	60 kg	Denitrification removal 0.07 – 0.11	Nizzoli et al. 2006
galloprovincialis	Italy		t N ha ⁻¹ yr ⁻¹ (Lab based study)	
Perna canaliculus	Kenepuru	Long lines	Denitrification removal 0.03 – 0.22	Kaspar et al. 1985
	Sound, New		t N ha ⁻¹ yr ⁻¹	
	Zealand			

Bivalves also immobilise or remove these nutrients through the production of biodeposits. These biodeposits increase the denitrification potential by providing anoxic environments for denitrifying bacteria (Newell *et al.* 2005). Denitrification transforms biologically available N and releases it to the atmosphere as either N2 or N2O which has been identified as an important removal mechanism for nitrogen in coastal waters (Piehler & Smyth 2011). This process makes it possible to limit the nutrient availability for algae and prevents aspects of eutrophication in the nearshore environment (Petersen *et al.* 2014).

There is a growing trend to use bivalves within integrated multi-trophic aquaculture (IMTA), initially starting in Asia (Fang et al., 2016) but the trend is now spreading globally. Fed aquaculture systems leak considerable amounts of nutrients to the surroundings, which could lead to eutrophication and deterioration of the environment. Large-scale intensive mariculture such as those in China, lead to undesirable biological and biochemical characteristics in coastal waters, which may have consequences on natural ecosystems (Liu and Su, 2017). Recently, the idea of using seaweeds and mussels as extractive species to clean the effluents from fish farms has grown considerably (Stedt, 2018). Bivalves are also themselves used to provide nutrients to assist in the culture of seaweeds within the IMTA systems (Fang et al., 2016). Using chemical or biological methods of nutrient removal from wastewater and in estuaries has proven to be expensive. As the concentration of nitrogen in wastewater becomes lower, the cost of removing it mechanically increases. It costs 6.20 kg^{-1} to reduce nitrogen to 8 mg l⁻¹, but \$19.13 kg⁻¹ to reduce nitrogen to 3 mg l⁻¹ (Evans, 2008; Rose *et al.*, 2014). Beseres Pollack et al. (2013) estimated that to remove 1 tonne of nitrogen it would cost \$8,996, while Newell et al., (2005) previously estimated it could be as much as \$31,050. Nutrient removal by bivalve harvest is being used as a Nature-Based Solution alternative to upgrading sewage works in Denmark (Petersen et al., 2014). In order to reduce the nutrient loads in Limfjorden by at least 5,700 tons of nitrogen per year, it was calculated that 9,500 ha of rope mussel aquaculture would be required, which would produce one million tonnes of mussel, although currently the 18.8 ha site is only producing 2000 tonnes. (Petersen et al., 2014). The running costs of this method of nutrient removal were estimated to be between 128,300-183,300 USD tonne⁻¹ N removed. This estimate does not include the potential income of selling the mussels, which are removed at a small size, and sold for chicken feed.

Phosphorus is one of the common elements on earth and is essential for all living organisms. Phosphate rock is the only economic source of phosphorus for the production of phosphate fertilizers and phosphate chemicals. Currently the reserves of phosphate rock are estimated at 40 billion tons and are found in the United States, China, Kazakhstan, Morocco, Finland, South Africa, and some Pacific Islands, but these reserves are estimated to run out in 60-130 years (van Ginneken *et al.*, 2016). Phosphorus recovery from wastewater, therefore, has grown in importance as it is a non-renewable resource and as well as that its discharge into the environment can cause serious negative impacts (Molinos-Senante *et al.*, 2011). Each human excretes around 1.5 grams of phosphorus per day into sewage, so with the current population of 6 billion an annual excretion of 3.3 billion-kilogram phosphate, which will increase to 5.5 billion-kilogram by 2050. Molinos-Senante *et al.*, (2011) found there was little economic incentive for the implementation of phosphorus recovery technologies because the selling price of rock phosphate is lower than phosphorus recovered from sewage. They calculated the shadow price of phosphorus, estimating it to be worth between \$13,118 – 58,561 tonne⁻¹ using a directional distance function to measure the environmental benefits obtained by preventing the discharge of phosphorus into the environment. Despite the current lack of economic incentive, van Ginneken *et al.*, (2016) clearly demonstrate that phosphorus recovery from the marine environment will increase in importance, and could be one of the most financially profitable aspects of bivalve aquaculture.

2.6.2 Biological accumulation of pathogens (regulation of biophysical environment, mediation of waste, biological accumulation)

Bivalves are filter feeders, and in areas of lower water quality can bioaccumulate bacteria, protozoa and viruses that are harmful to human health (Roslev *et al.* 2009; Clements *et al.* 2013). Oysters, mussels, clams and cockles are able to concentrate environmental elements and sewage related microbes within their tissues, (Alexander 1976; Daskin *et al.* 2008; Fukumori *et al.* 2008; Kovacs *et al.* 2010; Hassard *et al.* 2017). Several species of marine microalgae can produce toxins that enter the marine food web (Orr et al., 2013). In some cases, seafood contamination can provoke acute syndromes in human consumers, mainly through vectors such as bivalves. The most reputed syndrome originating from bivalve molluscs is paralytic shellfish poisoning (PSP), mainly due to its distinct neurological symptomatology and fatal outcome (Carvalho et al., 2019). This causes potential trade-offs with human consumption. However, due to the ability of bivalves to accumulate pathogens (Roslev *et al.* 2009; Clements *et al.* 2013; Aquatic Water Services Ltd 2014), bivalves could possibly be used as sacrificial beds to regulate and safeguard shellfish/finfish production locations, coastal waters and bathing beaches by accumulating pathogens before they reach them.

2.6.3 Carbon sequestration (regulation of biophysical environment, mediation of waste, sequestration)

Bivalve aquaculture is gaining widespread attention because of its role in the carbon cycle (Filgueira et al., 2015; Hickey, 2009; Tang et al., 2011; Waldbusser et al., 2013), due to the growing drive to mitigate climate change. Bivalves sequester carbon in the form of calcium carbonate via shell production (Hickey, 2009; Peterson and Lipcius, 2003). The average carbon in shell is 11.7% produced in the form of calcium carbonate although this varies between species (Error! Not a valid bookmark self-reference. Table-6). During the calcification process carbon dioxide is formed ($Ca + 2HCO_3 \rightarrow Ca CO_3 + CO_2 + H_2O$), so potentially leading to an increase in , pCO_2 in surface waters and evasion of CO_2 to the atmosphere – especially in the shallow well-mixed coastal waters where shellfish are typically farmed. Therefore, the calcification process is considered by some to be a source of atmospheric CO₂ (Fodrie *et al.*, 2017). Other authors argue that the C stored in shell represents a long-term sink. Hickey (2009) calculated the amount of carbon sequestered per year in oyster farms, using shell carbon content, spat weight, grow-out time and stocking density to be between 3.81 and 17.94 t C ha-¹ yr⁻¹. Higgins *et al.* (2011) created a model based on the results of CHN elemental analysis of tissue and shell, which estimated an oyster bed could remove a total of 13.47 ± 1.00 t C ha⁻¹ yr⁻ ¹ in a single growing season at a density of 286 oysters m⁻². These studies suggest a higher rate of carbon sequestration than other forms of blue carbon sequestration (Error! Reference source not found. Table 7). However, the long-term net effect on carbon storage is still unclear, and further work is required to look at the true potential of shellfish as a store of CO_2 .

Table 6 Chemical composition (carbon (C), nitrogen (N), phosphate (P)) (% dry weight) of shellfish, organised by species and average, minimum and maximum values. A dash indicates no value presented.

Species	Tissue			Shell			Reference
	С	Ν	Р	С	Ν	Р	
Oysters							
Crassostrea	-	8.4	-	-	-	-	Ren et al. 2003
gigas							
Crassostrea	44.90	8.19	-	11.52	0.12	-	Zhou et al.
gigas							2002
Crassostrea	-	7.4	-	-	-	-	Linehan et al.
gigas							1999
Crassostrea	44.72	7.72	0.83	12.17	0.2	0.04	Higgins et al.
virginica							2011
Crassostrea	-	7.54	0.99	-	-	-	Sidwell et al.
virginica							1973
Oyster mean	44.81±0.	7.85±0.1	0.91±0.08	11.845±0	0.16±0.04	0.04	
(±1 s.e.)	09	9		.33			
Mussels							
Mytilus edulis	45.98	11.40	0.708	12.68	0.55	-	Zhou <i>et al</i> .
							2002
Mytilus edulis	-	10.6	0.80	-	1.13	0.05	Haamer 1996
Mytilus edulis	-	8.1	1.24	-	-	-	Cantoni et al.
							1977
Mytilus	-	6.2	-	-	-	-	Miletic et al.
galloprovincia							1991
lis							

Mussel mean	45.98	9.075±1.	0.916±0.16	12.68	0.84±0.29	0.05	
(±1 s.e.)		19					
Other spp.							
Arctica	-	-	-	-	0.05	0.003	Westermark et
islandica							al. 1996
Chlamys	43.87	12.36	0.839	11.44	0.05	0.09	Zhou <i>et al</i> .
farreri							2002
Corbicula	-	9.81	-	-	0.22	-	Nakamura et
japonica							al. 1988
Mactra	42.21	10.57	-	11.52	0.19	-	Zhou <i>et al</i> .
chinensis							2002
Mactra	-	9.67	-	-	0.09	-	Hiwatari et al.
veneriformis							2002
Macoma	-	-	-	-	0.1	0.03	Seire <i>et al.</i>
baltica							1996
Musculista	-	-	-	-	0.82	0.05	Yamamuro et
senhousia							al. 2000
Pinctada	-	9.82	0.74	-	0.39	0.03	Gifford et al.
imbricata							2005
Pinctada	-	10.5	-	-	-	-	Seki 1972
imbricata							
Ruditapes	42.84	10.76	-	11.40	0.56	-	Zhou <i>et al</i> .
philippinarum							2002
Scapharca	45.86	8.71	-	11.29	0.07	-	Zhou <i>et al</i> .
suberenata							2002
Other spp.	44.35±0.	9.95±0.3	0.74±0.05	11.35±0.	0.46±0.08	0.04±	
Mean (±1 s.e.)	80	8		05		0.01	
Overall mean	44.86±0.	9.28±0.4	0.88±0.07	11.72±0.	0.32±0.09	0.04±	
(±1 s.e.)	54	0		19		0.01	

Table 6 continued.

Ecosystem type	Rate	of carbon	Number	of	References
	sequestratio	on	studies/sites		
	(t C ha ⁻¹ yr	¹)			
Salt Marshes	2.42 ± 0.26		50/143		(Ouyang and Lee, 2014)
Mangroves	2.26 ± 0.39		13/34		(Ouyang and Lee, 2014)
Seagrasses	1.38 ± 0.38		ND/123		(Ouyang and Lee, 2014)
Oyster Beds	13.47 ± 1.0	0	1/1		Higgins et al. 2011

Table 7 Carbon accumulation rates in different marine ecosystem types. ND – no data. Value ± SE Adapted from (Ouyang and Lee, 2014)

2.6.4 Reduced rates of shoreline and bed erosion (Mediation of flows, liquid and mass flows, hydrological cycle and water flow maintenance/Mass stabilisation and control of erosion rates)

Bivalve reefs and beds are able to protect the ecological integrity of other important habitats, such as seagrass beds and marshlands by providing protective structures (Turner *et al.* 1999; Scyphers *et al.* 2011). Many waterways suffer from the introduction of heavy shore defences due to the concentrated load upon soft sediments: the results of which can require additional efforts and funds in order to help maintain the breakwater structures (Piazza *et al.* 2005). Oyster reefs, however, act as biological barriers to reduce erosion, and do not require additional upkeep once established (Scyphers *et al.* 2011; La Peyre *et al.* 2015). Using data from multiple projects over an extended timeframe, La Peyre *et al.* (2015) found that oyster reefs reduced marsh retreat by an average of 1 m yr⁻¹ along moderately exposed and highly exposed shores. Location of the oyster reef barriers was crucial for ensuring their effectiveness, the oyster reefs requiring circulation currents suitable for larval recruitment and adequate water quality (Coen & Luckenbach 2000). While marshland retreat was not stopped, the rate of erosion was reduced (La Peyre *et al.* 2015).

2.7 Cultural services

Cultural ecosystem services are created by the interactions between humans and the natural world that enable the creation of cultural goods and benefits people obtain from an ecosystem. This interaction changes with time and can be modified through social and cultural influences, and human perceptions that involve memories, emotions and the senses (Church *et al.* 2014;

Jones *et al.* 2016). Cultural services offered by bivalve beds include recreational fisheries, historical artisanal fisheries for the public, education and tourism, seafood festivals and symbolic and spiritual benefits (Table 8).

Division Group		Class	Examples and indicative benefits
Physical and	Physical	Experiential use of	In situ wildlife watching (incl. aquatic
intellectual		animals and landscapes in	biodiversity) e.g. birds feeding
interaction with		different environmental	
biota, ecosystems		settings	
and land -	Intellectual and	Scientific, educational,	Subject matter for research and education
/seascapes representative		entertainment,	both on location and via other media.
	interactions	Heritage, cultural,	Historic records, cultural heritage; sense of
		aesthetic	place, artistic representations of nature.
			Seafood Festivals.
Spiritual, symbolic	Spiritual and / or	Symbolic	Emblematic animals.
and other	emblematic		
interactions with	Other cultural	Existence	Enjoyment provided by wild species,
biota, ecosystems,	outputs		wilderness, ecosystems.
and land-		Bequest	Willingness to preserve plants, animals,
/seascapes			ecosystems for the experience and use of
[environmental			future generations; moral/ethical perspective
settings]			or belief.

 Table 8 Cultural services of shellfish aquaculture using the CICES system for classification

2.7.1 In-situ wildlife watching (physical and intellectual interactions, physical, experiential use of animals)

Birdwatching, or birding, is a form of wildlife observation in which the observation of birds is a recreational activity (Cocker 2002). The number of people participating in this activity, and the contribution of bivalves to that activity via their influence on bird numbers are difficult to quantify and therefore value.

2.7.2 Education and research (physical and intellectual interactions, scientific, educational)

Some species of bivalves are frequently used for scientific experiments as they are hardy, fast growing, abundant and in the case of Mytilus edulis can reach sexual maturity in their first year (Ackefors & Haamer 1987). A literature search on Google Scholar and Web of Knowledge for

articles between 1918 and 2018 returns 511,000 results for shellfish, 254,000 for mussels, 210,000 for oysters and 196,000 for bivalves clearly showing the scale of research involving shellfish.

2.7.3 Heritage (intellectual and representative interactions)

Bivalves have an archaeological and historical value, with empty shells found in midden piles which have been dated to between 8,000 and 7,000 years (Rollins *et al.* 1987; Roosevelt *et al.* 1991). Among the indigenous peoples of the Americas who lived on the eastern coast, they commonly used pieces of shell as wampum (small cylindrical beads strung together). The shells were cut, rolled, polished and drilled before being strung together and used for personal, social and ceremonial purposes as well as currency (Dubin 1999). The Winnebago tribe from Wisconsin had numerous uses for mussels, using them as utensils and tools. They notched them to create knives and graters and carved them into fish hooks and lures as well as powdering shell into clay to temper their pottery. Shells were also used as scrapers for removing flesh from hides and scalping defeated enemies (Kuhm 2007).

2.7.4 Cultural (physical and intellectual interactions, heritage)

Seafood is a significant cultural element around the world, involving not just fishers but also distributors and the people who purchase shellfish for consumption. It is a traditional food at Christmas in France (Buestel *et al.* 2009), Italy and Spain. Seafood is commonly eaten in catholic countries on a Friday when red meat is not allowed. Fish and other aquatic animals are known to play an important role in the diet throughout the Asia-Pacific region. The wide range of fishery resources have given rise to a strong tradition of seafood eating in most countries of the region and this is reflected in strong cultural traditions associated with fish (Needham & Funge-Smith 2014). Bivalves have important representation in cultures around the world, with churches, sculptures and whole islands being created to celebrate them (Fig. 1). Bivalves have been mentioned in several songs such as 'Molly Malone' and 'the Oyster Girl', which mention the historic sale of oysters in Ireland.

2.7.5 Seafood festivals (physical and intellectual interactions, heritage, cultural)

Food has become a recognised component of cultural tourism globally, especially in rural regions (Lee & Arcodia 2011). Local foods or food products contribute to the authenticity of destinations, enhance the sustainability of tourism and strengthen the local economy. High quality food products from a specific region can enhance a region's overall tourism image and a visitor's experience (Boyne & Hall 2004). This tourism can provide economic stimulation to

a region while also maintaining or regenerating the local identity, especially through its primary production and processing sectors (Telfer & Wall 1996). Academic research is widening from a focus on the financial value and economic implications of food tourism (Belisle 1983; Telfer & Wall 1996) or its value as a promoting and marketing tool (Boyne & Hall 2004; Tellstrom \in *et al.* 2006), to include the cultural and social significance of a place (Hall & Gossling, 2016) and regional identity (Du Rand *et al.* 2003; Everett & Aitchison 2008). This change in approach demonstrates the increasing interest and importance of the social and cultural impacts of food tourism (Lee & Arcodia 2011). Food festivals are one tangible manifestation of this interest. 'Seafood Festivals' specialise this focus and are usually organised by local businesses with the aim of increasing local benefits to regional communities and businesses.

The reasons why people attend seafood festivals have not been fully investigated. One of the few reported was an evaluation of the Menai Seafood Festival, in North Wales, UK, (Lane & Jones 2016) found that 90% of respondents expressed their interest in purchasing local produce in the future, and the respondents were also encouraged by what they saw and experienced at the festival. Stallholder motivations for attending were mainly focused on the direct advantages for their businesses, such as promoting their products. Stallholders receive benefits in terms of high sales but also enjoy participating in the local event and supporting the surrounding community (Lane & Jones 2016). Estimates of economic value can be considerable. In the USA, the Louisiana seafood festival in 2015 attracted approximately 56,000 attendees and generated a total economic impact of \$1.75 million (Ortiz 2015). To provide some examples from around the world, seafood festivals in selected countries were identified using Google, Australia.com, everfest.com and foodfestivalfinder.co.uk. 120 were identified and contacted to find the number of visitors attending. Forty-nine responses were received from countries such as Australia, Jamaica, the Republic of Ireland, the United Kingdom and the USA, with an approximate attendance of ~1.4 million visitors (Appendix A – Table A 4).

2.7.6 Spiritual significance and emblematic (spiritual, symbolic and other interactions with biota)

There is a long historic spiritual significance of bivalves. In Roman times, it was believed that Venus, the goddess of love was born in the sea and emerged on a scallop shell towed by sea creatures. The Romans revered her and erected shines in their gardens, praying to her to provide water and verdant growth (Hoena 2003). Following the depiction of fertility and growth associated with the goddess of Venus, the scallop and other bivalve shells have come to be used as a symbol in architecture, furniture, fabric design (Fontana 1993), for example, within

the logo of the Royal Dutch Shell (the global oil and gas company). Scallops, whelks and other shells also feature as symbols in heraldry and coats-of-arms. The scallop is the symbol of St James and is called Coquille Saint-Jacques in French and it is an emblem carried by pilgrims on their way to the shrine of Santiago de Compostela in Galicia. Pilgrims that completed the pilgrimage were often buried with a scallop shell or had it carved on their tombs (Fulcanelli 1984). Scallop shells feature as a symbol in many churches in this region (<u>Figure 1Figure 1</u>).

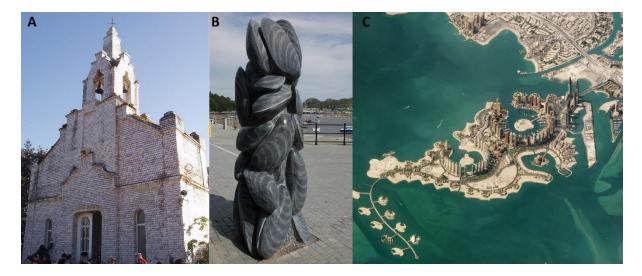


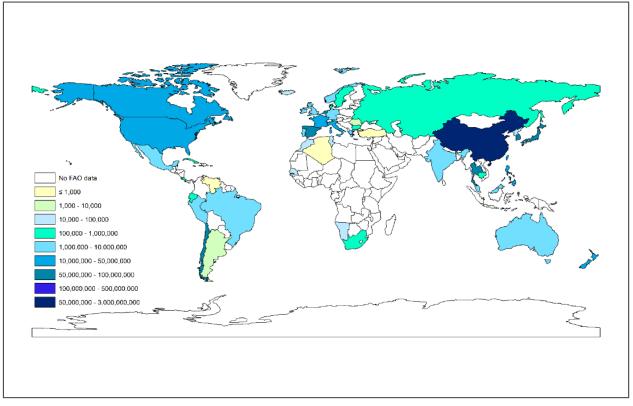
Figure 1 Examples of shellfish used in spiritual, emblematic or cultural contexts. A- The shell church, covered in scallop shells at La Toja, Spain; B- Sculpture of mussels in the mussel producing town of Conwy, Wales, UK; C- Hotel designed in the shape of an oyster: The Pearl, Qatar

2.7.7 Non-use (existence and bequest) values (other cultural outputs)

Bequest value is the value of satisfaction from preserving a natural environment or a historic environment for future generations (Turner & Schaafsma 2015). Shellfisheries are often important local centres of economic activity by fishers, local points of sale and wider distribution, nationally and internationally. A significant number of individuals may rely on the industry and a significant proportion of income in some coastal communities may rely on functioning shellfisheries. Often families are involved in this industry from generation to generation and therefore safeguarding shellfish waters from pollution can preserve these traditions (ECOTEC 2000). Hicks *et al.* (2004) suggested that people may benefit from oyster reefs in Chesapeake Bay even if they do not directly use the environmental asset. They achieve this by either deriving value from knowing that oyster reefs exist and provide ecosystem services or from knowing that improved environmental conditions might make future use of the bay more enjoyable should they choose to use the bay directly (Northern Economics 2009).

2.8 Global estimate of the potential value of nonmarket ecosystem services from bivalves

While the value of food from bivalve aquaculture is well reported (FAO 2016), the non-food ecosystem services are not. Therefore, using information collated in this study, global tonnages (Table 9) and their value (Table 10;<u>Error! Reference source not found.</u>Figure 2) were estimated. The services we were able to quantify and provide values for included nutrient (N and P) removal, and the use of oyster-shell waste as aggregate. Services that could not adequately be quantified, or value included: nursery grounds, bivalve use as fertilisers, pearls



and nacre, biological accumulation of E. coli

and other pathogens, and their influence in shellfish poisoning, shoreline defence, wildlife watching, use in education and research and the value of seafood festivals. This study estimated ecosystem services provided by bivalves based on the biomass removed at harvest (Table 9). While shellfish farms will have a larger standing stock, which will cycle nutrients during feeding and excretion, it is the harvested biomass that gives the most certain measure of nutrients removed from the marine system.

Figure 2 World map showing the potential combined value of carbon sequestration, nitrogen and phosphorus remediation and the use of oyster shells for aggregate (US\$).

Region	Tonnage of oyster shell waste	Nitrogen	Phosphorus	Total	Tonnage
	(t)	remediated (t)	remediated	Tonnage	of meat (t)
			(t)	(t)	
Africa	1,263	16	2	3,410	584
Americas	124,387	2,253	215	463,419	81,856
Asia	4,316,550	42,852	5,337	13,478,692	1,998,196
Europe	71,164	3,519	287	608,957	122,819
Oceania	12,513	549	46	95,054	19,306
World	4,525,876	49,210	5,886	14,649,532	2,222,762

 Table 9 Estimate of potential tonnages of constituents and chemicals within shellfish aquaculture production in 2015.

Global ecosystem services provided by bivalve aquaculture total \$30.39 billion (Table 10). Of these provisioning services (food) make up \$23.92 billion. Nutrient remediation has the potential to increase the global value of the bivalve industry by approximately \$1.20 billion. Oyster shell has the greatest potential value of ecosystem services globally. Annually 4.5 million tonnes of oyster shell is produced which has the potential to be used as aggregate, worth \$5.27 billion (\$2.43 billion–8.11 billion).

Bivalve production in Asia has by far the greatest potential ecosystem service value at \$26 billion, making up the majority (86%) of the global projection. Comparing between the various species produced globally (Table 11) it is clams, cockles and arkshells that are removing the most nitrogen (15,759 tonnes), and oysters removing the most phosphorus (2,408 tonnes). Mussels have the greatest potential for bioremediation as they remove the most nitrogen and phosphorus per tonne of shellfish produced.

Region	Value of food ecosystem	Value of using shell	Value of nitrogen	Value of	Total value of non-food	Total value of ecosystem
	services		remediation	phosphorus	ecosystem services	services
				remediation		
Africa	8,703	\$1,474	\$326	\$58	\$1,859	\$10,562 (\$9,551-11,572)
		(\$680 - 2,268)	(\$147 - 506)	(\$21-95)	(\$848-2,869)	
Americas	2,300,791	\$144,973	\$45,110	\$7,690	\$197,773	2,498,564 (2,390,793 -
		(\$66,920 -	(\$20,267 -	(\$2,815 -	(\$90,002 - 305,544)	2,606,335)
		223,026)	69,953)	12,565)		
Asia	19,983,869	\$5,030,939	\$858,033	\$191,280	6,080,252	26,064,121 (22,761,690 -
		(\$2,322,303 -	(\$385,500 -	(\$70,017 -	(\$2,777,821 -	29,366,552)
		7,739,574)	1,330,566)	312,543)	9,382,683)	
Europe	1,103,576	\$82,942	\$70,459	\$10,286	\$163,686	1,267,262 (1,177,283 -
		(\$38,286 -127,597)	(\$31,656 -	(\$3,765-	(\$73,707 -	1,357,241)
			109,262)	16,807)	253,665)	
Oceania	522,254	\$14,583	\$11,407	\$1,655	\$27,646	549,900 (534,717 - 565,084)
		(\$6,732 -	(\$5,125 -	(\$606 -	(\$12,463 -	
		22,435)	17,690)	2,705)	42,830)	
World	23,919,193	\$5,274,912	\$985,336	\$210,969	\$6,471,217	30,390,410 (26,874,035 -
		(\$2,434,923 -	(\$442,695 -	(\$77,224 -	(\$2,954,842 -	33,906,785)
		8,114,901)	1,527,977)	344,715)	9,987,592)	

 Table 10 Estimate of potential value of shellfish ecosystem services for shellfish aquaculture production in 2015 (US\$ 000).

Species	Tonnage of species	Potential nitrogen	Tonnes of nitrogen	Potential phosphorus	Tonnes of phosphorus	
	produced	remediation	removed	remediation	removed	
	through	(t)	tonne ⁻¹ of	(t)	tonne ⁻¹ of	
	aquaculture		shellfish		shellfish	
	(t)		harvested		harvested	
Clams. cockles,	5,395,188	15,759	2.92 x 10 ⁻³	1,567	2.90 x 10 ⁻⁴	
arkshells						
Mussels	1,856,300	12,370	6.66 x 10 ⁻³	913	4.92 x 10 ⁻⁴	
Oysters	5,316,345	12,399	2.33 x 10 ⁻³	2,408	4.53 x 10 ⁻⁴	
Scallops, pectens	2,081,699	8,682	4.17 x 10 ⁻³	998	4.79 x 10 ⁻⁴	

Table 11 Estimate of potential of bivalve nutrient remediation (t) between species for production in 2015

2.9 Knowledge gaps

The biological functions performed by bivalves are generally well-understood. However, there still remain knowledge gaps. For example, filtration rates of many species are not clearly reported, and the supporting ecological functions and trophic interactions supported by bivalves have only been studied extensively in the USA for one species: oysters. Therefore, for the supporting services, more basic quantification of processes is required to allow upscaling for other species and in other contexts. Although the value of oyster reefs acting as nursery grounds has been valued in the southeast United States (Peterson et al. 2003; Grabowski & Peterson 2007), these values are unsuitable for use in other parts of the world due to the difference in species and habitats. With a wider range of sites and species around the world assessed, it would be possible to better quantify the importance of this supporting service. The attempt to value provisioning services relies heavily on official statistics, which may underrecord what is being landed due to the contribution of small-scale and subsistence aquaculture (FAO 2016). There is no comprehensive data on use of shell in poultry grit, in aggregate, or of bivalve waste as a fertiliser, making it difficult to upscale on a regional or global basis. Due to the uncertainty in pearl value and the lack of valuation on nacre, these also have not been included in the global valuation.

Much of the information in bivalve regulating services is based on oysters in the USA and mussels in the Baltic, and their ability to remove nitrogen and phosphorus. The USA is also the only country with published estimates of their role in coastal protection. There is little data

from other regions in the world and for other species and it is uncertain whether nitrogen and phosphorus removal rates differ regionally/ globally. There is one study in the UK (Herbert *et al.* 2012) but this lacks in depth analysis on regulating services. More importantly, whilst some data on regulating services from Asia was found, there is relatively little data considering they are the largest producers of bivalves in the world. With regards to carbon sequestration, there remains disagreement in the literature on the net carbon storage attributable to carbonate in bivalve shells. Many of the values within this study refer to remediation or sequestration potential per hectare, however, the lack of information on the area of shellfish beds and their stocking densities makes it difficult to upscale to national or global potential from these studies.

Cultural services are among the most difficult to classify and value. Previously the cultural services of bivalve aquaculture have been largely ignored. To date there has been no published work into the cultural or economic importance of bivalve aquaculture, but with the growing interest in seafood festivals around the world, there is scope for the scale and value of some aspects of cultural services to be investigated. While it is difficult to value the existence and bequest value of bivalve aquaculture, it is an important aspect for both people involved in the industry and the wider population.

2.10 Conclusion

For the first time this study has valued on a global scale the ecosystem services provided by bivalve aquaculture. While the knowledge gaps summarised above currently hinder a comprehensive valuation, by using the values collated in this paper it is possible to make a partial estimate of the value of ecosystem services, including values for nutrient remediation and the use of oyster shell as aggregate. Worldwide these non-food services are worth \$6.47 billion (representing 27% of the current value for bivalve meat (FAO, 2016)). This shows that even without including the other services described in this synthesis, bivalve production areas have the potential to increase the overall value of the bivalve aquaculture industry globally, while simultaneously providing environmental benefits. Studies focused around the large estuaries of the USA and the eutrophic Baltic Sea show how significant bivalve aquaculture can be in terms of nutrient remediation, and nutrient offset schemes are being used in Denmark and Sweden (Petersen *et al.* 2014). Already there is a growing trend to use shellfish in integrated multi-trophic aquaculture due to their ability to remove nutrients and waste products from fed aquaculture. The benefit this could present to the farmer, could be through direct

payment for nutrient removal through a nutrient trading scheme, similar to the carbon trading schemes already in existence. While the carbon trapped in shell is considerable (1.06 M t yr⁻¹), it cannot be considered as a form of sequestration due to the CO2 released during calcification and respiration. Much of the extra value to non-food based ecosystem services, however, is in the use of shell as aggregate. Providing a market for the waste products of the industry. There remain gaps in this analysis due to lack of sufficient data, but it expected for these to further increase the overall value for ecosystem services provided by bivalve aquaculture. These include the prevention of shoreline erosion, increased biodiversity and the uses of bivalve waste, which have not been included in this valuation. Furthermore, while some estimates of non-use values, including existence, bequest and cultural values, are available for localised studies, there is insufficient data as yet to scale these into a global valuation. The analysis presented here can be used to indicate the likely scale of payments for ecosystem services provided by bivalve aquaculture, prior to more detailed assessments.

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3 Spatial variation in the carbon, nitrogen and phosphorus content of blue mussels, Mytilus edulis.

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3.1 Abstract

Shellfish farming can contribute to nutrient removal in coastal and estuarine systems, as bivalves directly incorporate nutrients into their tissues and shells. Mussels were collected at sites around the UK which had a range of annual water temperatures and a range of high and low catchment nutrient concentrations. CHN and phosphorus analysis showed that phosphorus in tissue had a significant negative relationship with mean annual seawater temperature for both rope and bottom cultured sites. Similarly, the percentage content of phosphorus in shell had a significant negative relationship with increasing salinity. Most notable was a significant difference between rope and bottom cultured mussels. Per tonne of live mussel, rope culture removed significantly more carbon (77.52 \pm 3.65 kg), nitrogen (8.50 \pm 0.59 kg) and phosphorus (0.95 \pm 0.07 kg) than bottom cultured (74.74 \pm 0.68 kg carbon, 5.00 \pm 0.013 kg nitrogen and 0.43 \pm 0.01 kg phosphorus). Further studies are required to account for the effect of growth, which could potentially increase the relative nitrogen and phosphorus remediation by rope culture compared to bottom culture even further than proposed here. These findings imply that the method of culture is amongst the most important aspects to consider when planning the use of mussels as nutrient remediators.

Keywords: Nutrient remediation, ecosystem services, regulating services, shellfish, bivalves

3.2 Introduction

Human activities have substantially increased the inputs of nutrients to coastal and estuarine waters (Boyer and Howarth, 2008) through increased use of chemical fertilisers in intensive agriculture and nutrient waste from expanding cities (Petersen *et al.*, 2019). Nutrients play significant biogeochemical roles in nearshore coastal and estuarine systems by controlling densities of micro- and macro-algae (Clements and Comeau, 2019; Gobler *et al.*, 2016; Rose *et al.*, 2014). Excess nutrients can lead to biogeochemical imbalance and substantial perturbation to coastal systems, leading to an increased occurrence of eutrophic estuaries around the world (Rose *et al.*, 2014).

In recent years mussel farms have been discussed as a mechanism of reducing the impact of terrestrial nutrient inputs to estuaries through their ability to filter phytoplankton and incorporate carbon (C), nitrogen (N) and phosphorus (P) into their shells and tissue (Clements and Comeau, 2019; Petersen *et al.*, 2019; Rose *et al.*, 2015) and nutrients being physically removed from the system when the mussels are harvested. N is considered the primary limiting factor in coastal environments, although P also encourages the growth of phytoplankton (Petersen *et al.*, 2019; Rose *et al.*, 2015). Mussels are filter-feeding organisms, and modify biogeochemical cycles by filtering large quantities of organic matter from the water column, which is used directly for growth and maintenance or is deposited on the sediment surface as faeces and/or pseudofeces (i.e. biodeposits) (Kellog et al., 2013).

To estimate the nutrient remediation potential of bivalve aquaculture, it is important to understand how different environmental conditions may influence the amount of C, N and P that can be removed. A range of environmental factors may influence mussel biology and potentially vary the capacity for N and P retention in tissue and shell. Temperature is a key factor which has long been understood to influence the metabolism of the blue mussel *Mytilus edulis* (Widdows, 1973), including filtration rates, absorption and the utilisation of available food (Zippay & Helmuth, 2012). *M. edulis* are more likely to grow faster or larger at warmer sites (Lesser *et al.* 2010), whereas low salinity has been shown to reduce filtration and growth rates of mussels, with faster growth in rope culture than bottom culture (Kamermans and Capelle, 2019). Food availability may also influence growth rates, and this is often represented by chlorophyll concentration (Rosland *et al.*, 2009; Thomas *et al.*, 2011). Suspended particulate material (SPM) has also been used as a proxy for food supply (Smaal and Haas, 1997), whilst

the tidal range has been used as a proxy for tidal velocity and hence water flow and food supply (Coen and Luckenbach, 2000).

There also appears to be a knowledge gap, as to whether the nutrient loading of the environment might influence the N and P retention of bivalves. As the environmental factors will vary spatially, there is a potential that the amount of nutrients removed could vary spatially as well. Additionally, increased catchment source nutrient loadings increases phytoplankton production in estuarine and coastal waters (Bricker *et al.*, 1999). This could also lead to variations in the concentrations of N and P in mussels at different locations. Mussels have the potential to optimize their nutrient balance by regulating food uptake quantitatively as well as qualitatively, and are able to store nutrients (Jansen *et al.*, 2012). This would imply that with increased food supply, it is possible mussels could have a resulting increase in N and P retention, although many factors influence mussel biology and, so, it is unlikely that this relationship would be linear.

As well as its role in nutrient remediation, bivalve aquaculture is also gaining widespread attention because of its potential role in the C cycle (Filgueira *et al.*, 2015; Hickey, 2009; Tang *et al.*, 2011; Waldbusser *et al.*, 2013), due to the growing drive to mitigate climate change. C is stored in the shells for long periods of time, and whilst some authors argue that the C stored in shell represents a long-term sink, others argue that due to biogeochemical transformations during the calcification process, particularly the CO₂ released into the water column, it should be considered to be a source of atmospheric CO₂ (Filgueira *et al.*, 2015; Fodrie *et al.*, 2017). Whether carbonate formation in bivalve shell is a net sink or a net source, it is still important to see how much C is stored in shell, and therefore removed from the marine system at harvest.

The UK is used as a case study for investigating the potential for shellfish farming in coastal nutrient remediation, due to the wide ranges of environmental and physical conditions including nutrient loading in catchments, sea surface temperatures, hydrodynamics, and coastal morphology. In Wales, Northern Ireland, The Wash, North Norfolk and Poole Harbour mussel production is mostly made up of bottom culture, within restricted Several Order fisheries, whilst rope grown mussels are produced in the UK, predominantly in Scotland, but also in Cornwall. Previous estimates of nutrient remediation by shellfish have used a single look-up value for tissue nutrient composition applied to data from many different environmental settings (e.g. (van der Schatte Olivier *et al.*, 2018). Typically, variation in tissue nutrient content due to regional or environmental factors has not been taken into account, although

some work has been carried out on oysters in eastern Canada (Clements and Comeau, 2019). Despite this, the role of environmental factors on nutrient composition in mussels is poorly understood. Therefore, this study aimed to investigate regional variation in C, N and P content in tissue and shells of *M. edulis* in estuaries around the UK, the potential mass of nutrients removed per tonne of mussels, and potential relationships with a range of environmental predictors such as estuarine nutrient loading, salinity, temperature and culture method.

3.3 Methods

3.3.1 Site selection

In order to assess potential variation in C, N and P contents of mussels due to environmental conditions, fourteen sites were selected around the UK (<u>Figure 3Figure 3</u>, <u>Table 12Table 12</u>). The sample sites were chosen to include a range of annual water temperature and a range of high and low catchment nutrient supply.

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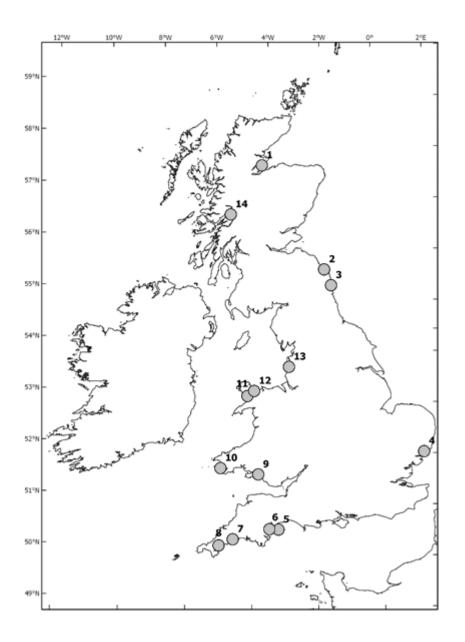


Figure 3 Map of sample sites around the United Kingdom. 1- Cromarty Firth, 2-Lindisfarne, 3- River Coquet, 4- Deben Estuary, 5- Lyme Bay, 6- River Teign, 7- River Fowey, 8- River Fal, 9- Swansea docks, 10- Milford Haven, 11- River Braint, 12- Menai Strait, 13- River Ribble, 14- Loch Leven

Suitable sites were chosen based on shellfish production area reports (CEFAS, available from https://www.cefas.co.uk/data-and-publications/sanitary-surveys/scotland/ and

<u>https://www.cefas.co.uk/data-and-publications/sanitary-surveys/england-and-wales/reports/</u>) selecting estuaries where blue mussels (*M. edulis*) were present. Sites were at both bottom cultured sites (intertidal), and on rope systems (subtidal). Site sea surface temperature and chlorophyll-a values was found from satellite imagery using the Copernicus Marine

Environment Monitoring Service (CMEMS, available from http://marine.copernicus.eu/). Average concentrations of nitrate in the input rivers to each estuary were estimated from data in the harmonised river monitoring scheme (HRMS, available from https://data.gov.uk/dataset/bda4e065-41e5-4b78-b405-41c1d3606225/historic-uk-waterguality-sampling-harmonised-monitoring-scheme-summary-data). SPM data were obtained from satellite images available at http://data.cefas.co.uk/#/View/18133 (Silva et al., 2016). Tidal range was obtained from the Enhanced UK Estuaries Database (Manning and Whitehouse, 2012).

Table 12 Site characteristics of 14 selected sampling locations (<u>Figure 3</u> Figure 3). All data except tidal range represent annual means. * indicates a wild bed. ⁺ indicates subtidal mussel culture.										
ID	Site name	Seawater	Nitrate	river	Chlorophyll-a	Tidal	salinity	Suspended	Culture method	

ID	Site name	Seawater	Nitrate river	Chlorophyll-a	Tidal	salinity	Suspended	Culture method
		surface	concentration	(mg m ⁻³)	range	(ppt)	particulate	
		temperature	(mg l ⁻¹)		(m)		matter (mg l ⁻	
		(°C)					1)	
1	Cromarty Firth	8.2	0.11	2.20	2.62	32.9	1.78	Bottom
2	Lindisfarne*	9.1	3.68	1.49	3.16	33.5	7.55	Bottom
3	River Coquet*	9.0	0.25	1.62	3.04	33.6	5.20	Bottom
4	River Deben*	11.5	11.50	3.70	2.24	33.7	58.68	Bottom
5	Lyme Bay ⁺	12.9	4.35	0.84	2.60	35.1	3.14	Rope
6	The Teign	12.6	2.03	3.26	2.64	34.0	2.43	Bottom
7	River Fowey ⁺	12.4	1.82	1.05	3.40	34.6	2.12	Rope
8	River Fal*	12.6	3.43	1.25	3.42	34.4	1.70	Bottom
9	Swansea Docks ⁺	11.8	0.73	1.91	6.34	29.5	7.42	Rope
10	Milford Haven*	11.9	3.25	0.95	4.46	33.4	6.55	Bottom
11	Afon Braint*	11.0	2.5	2.13	3.02	32.9	8.09	Bottom
12	Menai Strait	10.8	0.60	4.50	5.14	30.3	6.48	Bottom
13	River Ribble*	10.6	4.73	2.17	6.16	27.8	23.46	Bottom
14	Loch Leven ⁺	9.6	4.73	1.61	3.70	28.0	0.96	Rope

3.3.2 Sample collection

Preliminary analysis was conducted at two of the survey sites: Menai Strait and Afon Braint, to assess between-individual and between-location variation, to develop the sampling strategy for the multi-site survey. Following this in September and October of 2018, it was found that five random locations around each site and six mussels were needed from each location to account for within-site variation. Mussels were chosen that were between 40-90mm in length to represent mussel size at harvest.

3.3.3 Sample preparation

After collection, mussel shells were scraped clean of encrusting barnacles, patted dry using paper towels and the live weight was taken before the shell length was obtained using digital Vernier callipers. The mussels were placed in labelled zip lock bags before being frozen to -20°C prior to analysis. In the laboratory, the mussels were defrosted, and the tissue completely removed from the shell. The wet weight of tissue was determined after gently rolling samples in paper towel to remove excess external water. Tissue samples were placed into tin dishes and frozen to -20°C before being placed in a freeze dryer for 120 h at a vacuumed temperature of -40°C. Once completely dry, the dry weight was taken. The mussels were hand-ground with a pestle and mortar and then placed into Precellys tubes with stainless steel ball bearings and ground to a fine powder. The tissue of the six mussels from each location were pooled and homogenised, creating five replicate samples to be analysed from each site.

Shells from the pooled samples of six mussels were patted dry using paper towels and wet weight taken, then oven dried at 60°C for 120 h and dry weight taken. The dried shells were crushed with a hammer into small pieces, then placed in a hammer mill and ground to 1mm particles, and finally ground to a fine powder in a ball mill.

3.3.4 Elemental analysis

Nutrient analysis was based around the methods of Higgins et al. (2011) and Zimmermann and Keefe (1997). N and C content was measured in subsamples of dried tissue and shell, using a Flash elemental analyser, with flash combustion (950°C) and measurement of gaseous products by gas chromatography. The dry weights of samples analysed were between 1 to 1.5 mg for tissue, and 9.5 to 10.5 mg for shell. Optimum sample weights were determined prior to analysis. All samples were run with carrier gas blanks, sample blanks (empty tin capsules), a duplicate sample, then acetanilide standards following every ten samples run. Each day samples were run Apple leaves NIST 1515 and NIES mussel tissue were run to ensure the machine-

maintained accuracy. There was no observed drift in the calibration with time, and so elemental composition was calculated based on a mean for all blanks and acetanilide standards.

3.3.5 Phosphorus analysis

Phosphorus analysis was based on the methods of Solórzano and Sharp (1980). Mussel shell and tissue samples were weighed out into porcelain crucibles (100mg of tissue and 2g of shell), as well as samples of Certified Reference Material -BCR-684 (sediment). The samples, reference materials and blanks were placed in a muffle furnace for 3 hours at 450°C. Once cooled, samples were placed in centrifuge tubes and acidified with 10 ml of 3.5 M HCl. If any sample remained in the crucible, they were rinsed with further aliquots of 3.5 M HCl and the final volume made up to 20ml. These were placed on an orbital shaker for 16 hours, before centrifugation at 3000 rpm for at least 15 minutes or until all the supernatant was clear. 10 ml of the supernatant was pipetted into a 50 ml falcon tube.

To make a stock phosphate solution of 1000 mg per litre, 0.439 g of anhydrous KH_2PO_4 was dried overnight in an oven at 60°C. This was then dissolved in 100 ml of deionised water (DI water) and a range of standards from 0-100 ug l⁻¹ were used to create a calibration curve. Each standard had 10ml of 3.5 M HCl added, followed by 5 drops of Nitrocresol (4-Methyl-2-nitrophenol, C₇H₇NO₃, 0.25%). Each of the standards was then de-acidified with 9.5ml of 5M NaOH. If the solution did not change from a pale, clear yellow, then 0.5 ml of 5 M NaOH was added at a time until the solution darkened. The standards were then topped up to 50ml with DI water.

A colour developing reagent was made up with 50ml H_2SO_4 (2.5 M or 13 %), 5ml potassium antimony tartrate ($C_8H_{10}K_2O_{15}Sb_2$) solution (0.27 %), 15ml ammonium molybdate solution ((NH_4)₆Mo₇O₂₄) (10g in 100ml of DI water) and 30ml ascorbic acid ($C_6H_8O_6$) (1.76g in 100ml of DI water). 5 ml of each neutralised standard was pipetted into a clear plastic test tube, then 3 ml of DI water and 2 ml of colour developing reagent was added to each tube. These were allowed to stand for 15 minutes until the colour had developed and were analysed within one hour. The solution was then poured into 1.6 mm disposable UV cuvettes and measured using a spectrophotometer (Evolution 201). The 10 ml of the supernatant in the 50 ml falcon tube had 5 drops of Nitrocresol added. Each was then de-acidified with 9.5ml of 5M NaOH. If the solution did not change from a pale, clear yellow, then 0.5 ml of 5 M NaOH was added at a time until the solution was then pipetted into a clear plastic test tube, then 7ml of DI water and 2 ml of colour developing reagent was added to each tube. These also were allowed to stand for 15 minutes and analysed within one hour before being analysed with the spectrophotometer (Evolution 201 Spectrophotometer).

3.3.6 Statistical analysis

3.3.6.1 Percentage carbon, nitrogen, and phosphorus analysis

Linear models (S1, Supplementary material) were used to explore which factors explain variation. The Shapiro–Wilk test was used to test for normality and the Levene's test for homogeneity of variance in C, N and P content of mussels. Percentage P in tissue was log transformed in order to meet the assumptions of normality. Variables were tested for collinearity using Pearson correlation. SPM was highly correlated with annual nitrate (greater than 0.80 (Garson, 2012) and therefore SPM was removed from the model.

A linear model was then prepared accounting for all the environmental variables still included following the collinearity checks, all were continuous variables with the exception of culture type which was a categorical variable. The best model was selected using the dredge function from the Package MuMIn (version 1.43.6). This function selects the lowest Akaike information criterion (AIC) score and a delta AIC score below 2 (Burnham and Anderson, 2004). Following the linear model an ANOVA F-test was carried out to test the significance of each variable. Post model validation was carried out using QQ plots and residuals vs fitted graphs (Zuur *et al.*, 2010).

3.3.6.2 Upscaled values of kg per tonne of harvested live weight

The percentage C, N, and P can give different results to the kg of C, N, and P tonne⁻¹ of live mussels, due to variation in the proportion of tissue and shell in mussels around the UK. To find the mass of C, N and P tonne⁻¹ of live mussels, the percentage contents were upscaled to values per tonne of live mussels using the conversion factors derived from the live weight, wet weight and dry weight of each component (shell and tissue) measured during processing using the following formulae.

Dry Weight per tonne⁻¹ of mussels (kg) = $\frac{Average dry weight of animal (g)}{Average Live weight of animal (g)} \times 1000 \text{ kg}$ Dry Shell (kg) per tonne⁻¹ of mussels (kg) = $\frac{Average Shell dry weight (g)}{Average dry weight of animal (g)} \times Average dry weight (kg)$

Dry Tissue (kg) per tonne⁻¹ of mussels (kg) = Average dry weight of animal (kg) – Average Dry shell weight (kg)

This was calculated for the five locations at each site and then averaged for each site. The data were then analysed using linear models, with model selection carried out as above and significance of each variable tested ($p \le 0.05$), using the ANOVA F-test.

All statistical analyses were conducted using R 3.5.2 (R Foundation for Statistical Computing 2011).

3.4 Results

3.4.1 Percentage content nitrogen, and phosphorus analysis

Percentage C, N, and P content in mussel tissue was much higher than that of shell (<u>Table 13</u>). Furthermore, tissue content was also more variable than that of shell for all the response variables. The highest range was recorded for tissue percentage C content (38.77% to 45.69%), followed by tissue percentage N content (7.86% to 10.22%), while tissue percentage P content had the lowest range (0.87% to 1.41%). In contrast, the variability of shell nutrient content was much lower, shell percentage C content (12.48% to 13.54%), shell percentage N content (0.28% to 0.78%), while tissue percentage P content had the lowest range (0.009% to 0.018%).

There was significantly higher percentage C and P content in the tissue of rope cultured mussels (Effect of culture method, GLM, $p \le 0.05$, Figure 4A and 4C) compared with bottom cultured mussels (43.50 ± 0.48 %C, 1.30 ± 0.07 %P and 40.97 ± 0.20 %C, 1.03 ± 0.03 %P, respectively). There was no significant difference in percentage N content in the tissue of rope cultured mussels and bottom cultured mussels (Figure 4B). There was significantly higher percentage content of C and N in shell of rope cultured mussels (Effect of culture method, GLM, $p \le 0.05$, Figure 4D and 4E) compared to bottom cultured mussels (13.10 ± 0.08 %C, 0.59 ± 0.03 %N and 12.70 ± 0.04 %C, 0.42 ± 0.02 %N, respectively). However, there was no difference in the percentage P content in shells of rope and bottom cultured mussels (Figure 4F).

There was a significant negative relationship between percentage P content in tissue and mean annual seawater temperature (Effect of mean annual seawater temperature, GLM, $p \le 0.05$), for both rope and bottom cultured mussels separately (Figure 5C). There was also a significant negative relationship between percentage P content in shell (Effect of mean annual salinity,

GLM, $p \le 0.05$), when data from both rope and bottom cultured sites were pooled (Figure 6F). There was no significant effect of seawater temperature or salinity on the percentage C and N content in either tissue or shell. The average annual nitrate load of the survey sites varied from 0 to 6 mg l⁻¹, with the exception of the Deben estuary having an exceptionally high nitrate load of 11.5 mg l⁻¹. However, there was no significant relationship between mean annual nutrient concentration and the percentage C, N, and P content in mussel tissue or shell (Figure 7).

ID	Site name	Percent	Percent		Percent	Percent	Percent	Percent
		carbon i	n nitrogen	in	phosphorus in	carbon in	nitrogen in	phosphorus in
		tissue	tissue		tissue	shell	shell	shell
1	Cromarty Firth	43.01±0.17	9.65±0.09		1.18±0.07	12.54±0.06	0.38±0.026	0.010±0.001
2	Lindisfarne	38.77±0.27	8.25±0.07		1.24±0.09	12.35±0.07	0.28±0.03	0.012±0.001
3	River Coquet	40.72±0.23	8.42±0.06		1.15±0.10	12.88±0.10	0.53±0.04	0.012±0.000
4	Deben Estuary	40.18±0.19	8.25±0.07		0.95±0.07	12.71±0.12	0.46±0.06	0.013±0.001
5	Lyme Bay +	44.78±0.22	8.89±0.09		1.00±0.03	12.92±0.05	0.55±0.02	0.012±0.001
6	River Teign	40.37±0.13	8.16±0.04		0.89±0.08	12.78±0.18	0.46±0.06	0.012±0.001
7	River Fowey +	42.98±0.46	10.22±0.14		1.61±0.09	12.74±0.10	0.45±0.04	0.009±0.000
8	River Fal	41.38±0.42	8.67±0.10		1.05±0.14	12.93±0.06	0.54±0.03	0.015±0.002
9	Swansea Docks +	40.53±0.44	8.46±0.17		1.16±0.15	13.19±0.07	0.56±0.07	0.013±0.001
10	Milford Haven	40.06±0.29	8.63±0.13		0.89±0.03	12.48±0.06	0.31±0.03	0.013±0.001
11	Afon Braint	41.67±0.29	8.27±0.09		1.09±0.05	12.53±0.05	0.31±0.02	0.015±0.002
12	Menai Strait	40.72±0.59	7.86±0.12		0.97±0.01	12.96±0.06	0.51±0.01	0.015±0.001
13	River Ribble	43.07±0.24	9.22±0.09		0.87 ± 0.06	12.69±0.21	0.43±0.09	0.012±0.001
14	Loch Leven +	45.69±0.32	8.57±0.07		1.41±0.14	13.54±0.06	0.78±0.27	0.018±0.002
	Overall Mean ±SE	41.71±0.24	8.68±0.08		1.10±0.033	12.80±0.04	0.47±0.02	0.013±0.001

Table 13 Percentage (%) composition of carbon, nitrogen and phosphorus present in sampled mussel shell and tissue from the 14 sampled sites and overall mean. Cell values are mean \pm SE of five sampling locations per site. + indicates rope cultured mussels.

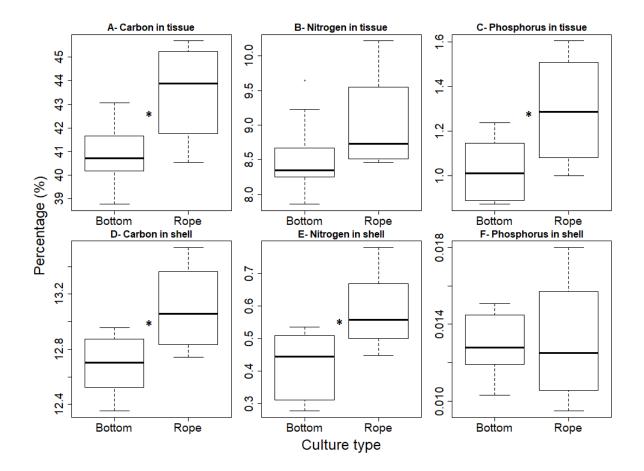


Figure 4 A comparison of the percentage (%) of (A,D) carbon, (B,E) nitrogen, and (C,F) phosphorus present in the sampled mussel tissue (top row) and shell (bottom row). The boxes indicate the 25th and 75th percentiles, median (thick line), error bars indicating the 1.5 times inter-quartile range. The asterisks indicate a significant difference between culture methods. *GLM, $p \le 0.05$.

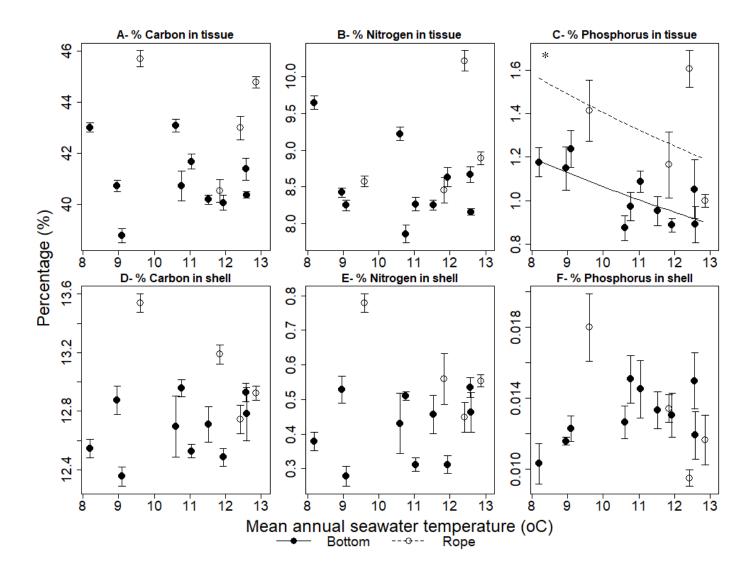


Figure 5 The percentage (%) of (A, D) carbon, (B, E) nitrogen, and (C, F) phosphorus (with SE bars) present in the sampled mussel shell against the mean annual temperature (°C). Lines on graph indicate significant linear relationships. *GLM, p \leq 0.05. Filled circles and solid lines represent bottom cultured mussel sites (log y = -0.586x + 0.648) and empty circles and dashed lines represent rope cultured (log y = -0.568x + 0.927).

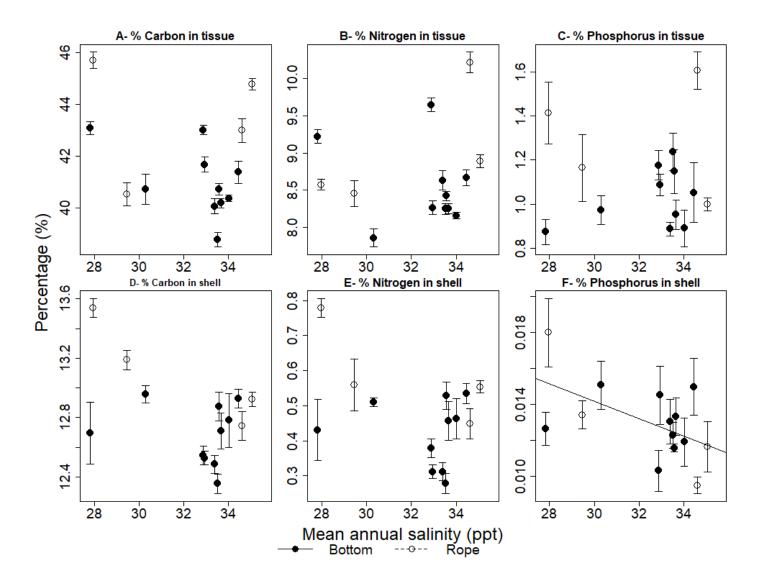


Figure 6 The percentage (%) of (A, D) carbon, (B, E) nitrogen, and (C, F) phosphorus (with SE bars) present in the sampled mussel shell against the mean annual salinity (ppt). Filled circles represent bottom cultured mussel sites and empty circles represent rope cultured sites. Line on graph indicate significant linear model relationship for pooled bottom and rope culture (3F, line equation y = -0.0005x + 0.029).

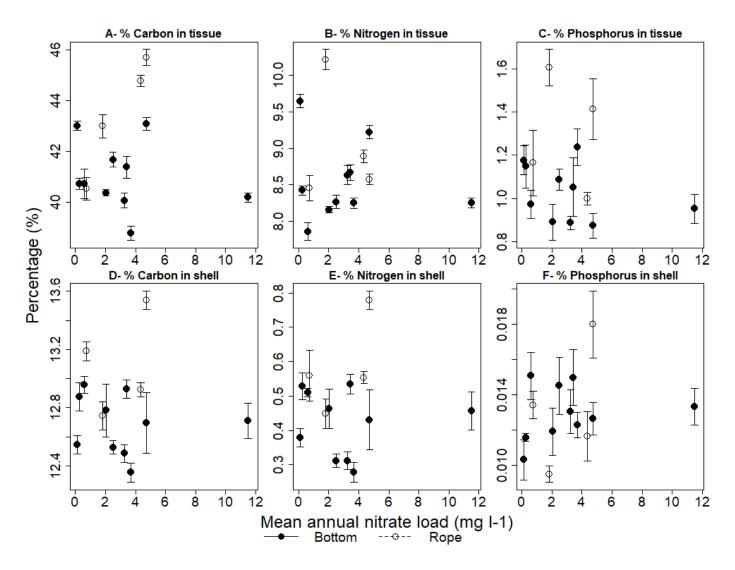


Figure 7 The percentage (%) content of (A, D) carbon, (B, E) nitrogen, and (C, F) phosphorus (with SE bars) present in the sampled mussel shell against the average catchment annual nitrate load (mg l-1) from the 14 sampled sites.

3.4.2 Kg of nutrient per tonne of live mussel

When expressed as a proportion of total weight of live mussel (kg tonne⁻¹), culture method was found to have a significant effect on the kg of C, N, and P in tissue and shell (GLM, $p \le 0.05$, Figure 8, Appendix B). The C kg tonne⁻¹ in tissue of rope cultured mussels (31.40 ± 2.88 kg) was double that in bottom cultured (14.59 ± 0.55 kg, Figure 8A). Conversely, the C kg tonne⁻¹ in shell of bottom cultured mussels (60.15 ± 0.77 kg) was significantly higher than in rope cultured (GLM, $p \le 0.05$, 46.12 ± 1.69 kg, Figure 8D). However, overall, there was no significant difference in the C kg tonne⁻¹ of rope cultured (77.52 ± 3.65 kg) and bottom cultured mussels (74.74 ± 0.68 kg, Figure 8G).

The N kg tonne⁻¹ in tissue of rope cultured mussels (6.48 ± 0.58 kg) was also double that of bottom cultured (14.59 ± 0.55 kg, Figure 8B). There was no significant difference in the N content of shell between bottom and rope cultured mussels (Figure 8E). Overall, there was significantly more N kg tonne⁻¹ in rope cultured (GLM, p ≤ 0.05 , 8.50 ± 0.59 kg) than bottom cultured (5.00 ± 0.013 kg, Figure 8H).

The P kg tonne⁻¹ in tissue of rope cultured mussels $(0.90 \pm 0.07 \text{ kg})$ was significantly higher than that of bottom cultured (GLM, p ≤ 0.05 , 0.69 ± 0.01 kg, Figure 8C). In shell, bottom cultured mussels $(0.06 \pm 0.001 \text{ kg})$ had significantly more P kg tonne⁻¹ than that of rope cultured (GLM, p ≤ 0.05 , 0.04 ± 0.001 , Figure 8F). Overall, there significantly more P kg tonne⁻¹ in rope cultured (GLM, p $\leq 0.05, 0.95 \pm 0.07$ kg) than bottom cultured (0.43 ± 0.01 kg, Figure 8I).

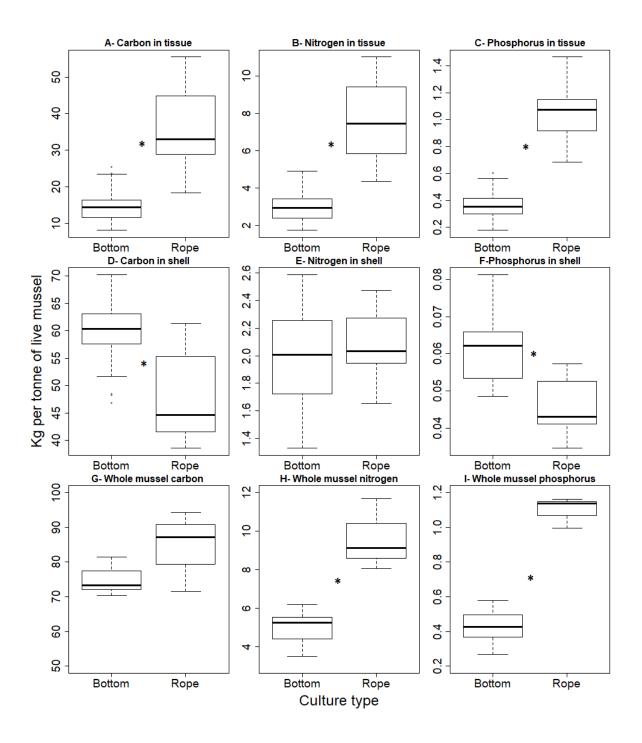


Figure 8 A Comparison of kilograms (Kg) of carbon (A, D, G), nitrogen (B, E, H), and (C, F, I) phosphorus per tonne of live mussel harvested. The boxes indicate the 25th and 75th percentiles, median (thick line), error bars indicating the 1.5 times inter-quartile range. The asterisks indicate a significant difference between culture methods. * GLM, $p \le 0.05$.

3.5 Discussion

Several studies have highlighted mussels as a potential mechanism for removing excess nutrients from eutrophic estuaries (Timmermann *et al.*, 2019; van der Schatte Olivier *et al.*, 2018), with the focus being split between net storage of nutrients within the mussel shell and tissue (Petersen *et al.*, 2016), and chemical reactions such as denitrification in the sediments beneath mussel beds (Carlsson *et al.*, 2012). The removal of whole animals presents a clear, calculable quantity of nutrient removal, although Mcleod and Mcleod (2019) also highlight the need for site specific assessments to be carried out in order to gain site specific values for C, N and P. This study aimed to calculate C, N, and P values in whole organisms and tissue and shell in order to better understand whether and how these vary in response to environmental factors. This study showed that average annual seawater temperature and salinity did influence the P content of mussel's tissue and shell respectively. Average annual nutrient loading, annual mean chlorophyll-a, and tidal range were found to have no influence. This study has shown that a crucial factor to take into account when assessing the potential of C and nutrient removal services is the culture method used, with rope cultured mussels removing significantly more N and P than bottom culture.

The significant negative relationship between P in tissue and temperature suggests that mussels in cooler waters have a higher percentage content P in tissue. Previous work by Widdows (1973) found that as water temperatures increased over a range from 5°C to 20°C, there was an increase in metabolism and oxygen uptake. Relatedly, Smaal and Vonck (1997) found respiration rates showed a seasonal pattern, with high values in early spring and summer, and relatively low values in autumn and winter. Their study also found that in the summer and autumn, there was relatively low P content, but this increased over winter and into spring, potentially due to a temperature effect on metabolism.

The significant negative relationship between P in shell and salinity suggests that the ability to remove P through shell production will be more efficient in systems with lower salinity. Studies have found reduced growth with decreasing salinity, therefore mussels in lower salinity environments will generally be smaller (Riisgård *et al.*, 2012). Mussel shells are primarily composed of CaCO₃ (95–99% of CaCO3 as aragonite) but can also contain phosphate (P₂O₅) in the periostracum layer (Miculescu *et al.*, 2018). The periostracum is a thin organic coating which is the outermost layer of the shell (Taylor and Kennedy, 1969). Therefore, mussels with

thicker shells, could account for a larger percentage of the total shell mass, and hence lower P content in homogenised shell samples. In this study, mussels were selected within the normal commercial size range to compare between sites, these were then homogenised for analysis, therefore removing the ability to analyse the effect of mussel size on P content. Despite this, P in shell only contributed a small amount of total P, with the majority being removed in tissue. These effects may have implications for using shellfish as a tool for nutrient removal in regions where coastal waters are cooler and less saline (Carlsson *et al.*, 2012; Petersen *et al.*, 2014).

The most influential factor on potential for nutrient remediation was the culture method used. Globally bottom culture, only accounts for approximately 15% of overall mussel production, with suspended and off-bottom culture, accounting for around 85% (McKindsey *et al.*, 2011). Comparatively the UK does not follow this trend, with more bottom culture than rope. Due to lower predation pressure on rope cultured bivalves (Kamermans and Capelle, 2019), there is less energy put into shell production and an increased production of meat. As the tissue contained the highest proportion of nutrient, this led to significantly higher N and P content (kg tonne⁻¹) in rope cultured mussels.

Despite this only C incorporated in shell can be considered a long-term C store (Mangerud and Gulliksen, 1975), whilst the tissue is consumed and respired. This study found that despite having a similar weight of C removed at both bottom and rope cultured mussels, there was significantly more C removed in shell at bottom cultured sites. Previous work has shown that mussels grown subtidally have thinner shells than those grown in the intertidal zone (Beadman *et al.*, 2003). Despite the ongoing debate of whether shellfish act as a method of C sequestration (Filgueira *et al.*, 2015), it is still useful to estimate the tonnage of C being taken out of the system at harvest. This indicates that if mussels were to be used as a method to capture C, it would be best achieved through bottom culture.

Bottom culture is typically regarded as the least efficient method for culturing mussels, due to the high density dependent losses (Cubillo *et al.*, 2012) and predation pressure (Capelle *et al.*, 2017). Kamermans and Capelle (2019) summarised several studies and there was a large variance in the areal density of mussels produced on ropes, with an average of 69.6 kg m², whilst bottom aquaculture has been shown to produce an average 6.4 kg m². This could be explained as rope grown mussels are subtidal, whilst bottom grown mussels in the intertidal zone less stable growing conditions, with sigificant temporal variations in temperature, water

pressure and sunlight radiation. Mussels grown on rope are not exposed to air, grow faster and are able to reach more essential <u>nutrients</u> from the water and are buffered from extreme changes in temperature (Tagliarolo et al., 2012).

Combined with the higher nutrient content of rope-grown mussels, this would indicate that future developments for nutrient remediation would look to utilise suspended rope mussel aquaculture due to the potential higher nutrient yield per area. As intertidal sites have limited potential, moving mussel farming offshore would seem the logical next step, with large offshore sites already being developed off the south coast of England (Sheehan *et al.*, 2020).

The present study has shown that culture method has a significant effect on the potential C, N, and P removal by mussels. It also highlights that differences in temperature and salinity can also influence retention of P removal in tissue and shell, respectively. Other studies have shown that both of these can also affect growth rates (Riisgård et al., 2012; Mackenzie L Zippay and Helmuth, 2012), and therefore time to harvest on mussel farms. This would also be an important factor should mussels be used as a tool for dealing with nutrient remediation. Warmer waters facilitate faster growth, therefore a shorter period from seed to harvest. Thus, whilst our findings show that warmer temperatures will have a negative relationship with P content in tissue, this could be offset by the higher rate of nutrients removal due to the faster production cycle. This would require further modelling of nutrient uptake and retention with growth and the reproductive cycle in order to confirm.

3.6 Conclusions

The findings of this study show that when planning a large-scale policy approach to using mussels as nutrient remediators, the most important factor to consider is the method of culture. Rope cultured mussels removed double the amount of N and P per tonne harvested compared to bottom cultured mussels. Our calculations do not account for growth rates, which previous studies have shown are faster in rope cultured mussels than bottom cultured. This could potentially further increase N & P remediation by rope culture. While average seawater temperature did not influence nutrient content of mussels positively, it should, be noted that warmer temperatures will support faster growth and therefore a higher rate of nutrient removal. Similarly, while there is more C trapped in the shell of bottom cultured mussels, this may be offset by the greater growth rate expected in rope-cultured mussels.

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4 Temporal variation in the carbon, nitrogen and phosphorus content of blue mussels, Mytilus edulis at a high and low nutrient site.

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This paper has not been published, but is in preparation for publication. The PhD candidate carried out all work, analysis and writing.

4.1 Abstract

There is a growing recognition of the wider ecosystem benefits of bivalve aquaculture in coastal waters, including regulating services such as carbon sequestration and nutrient remediation. While other studies have investigated spatial and site-specific data on nutrient retention in shellfish, the management of shellfish harvesting to optimise nutrient sequestration, there remains the need for a better understanding of seasonal patterns of nutrient content. This study compares temporal changes in carbon, nitrogen, and phosphorus percentage content as well as the upscaled values, taking into account whole mussels across two contrasting estuaries, to investigate the removal potential through mussel aquaculture. The kg of nitrogen and phosphorus per tonne of mussels was highest before spawning at both sites. The period immediately after spawning, and across the summer (May-August) had the lowest nutrient levels within the mussels, before the sites recovered over autumn and winter. In agreement with previous findings, the seasonal changes observed in tissue condition followed the patterns of their reproductive cycle. Most nutrient removal of nitrogen and phosphorus was carried out by the tissues, with a small amount removed in shell. Our findings provide evidence that harvesting directly before spawning or once the mussels had recovered following spawning, provides the most effective nutrient remediation. This study has found that mussels which are found more subtidally, have greater potential as nutrient remediators than intertidal mussels higher up the shore.

Keywords: Nutrient remediation, ecosystem services, regulating services, shellfish, bivalves

4.2 Introduction

In recent years mussel farms have been discussed as a mechanism of reducing the impact of terrestrial nutrient inputs to estuaries through their ability to filter phytoplankton and incorporate carbon (C), nitrogen (N) and phosphorus (P) into their shells and tissue (Petersen *et al.*, 2019; Rose *et al.*, 2015; van der Schatte Olivier *et al.*, 2018).

Algal blooms occur naturally, however, human activities have substantially increased nutrient inputs to coastal and estuarine waters, resulting in nutrient pollution and a global increase in eutrophication (Boyer and Howarth, 2008). Policy efforts over the last 20 years in Europe have improved water quality in most estuarine areas (Billen *et al.*, 2011), and the UK does not suffer from frequent eutrophic events (Maier *et al.*, 2009), in contrast to the Baltic (Stadmark and Conley, 2011) and the United States of America (Howarth and Paerl, 2008). However, as sea temperature increases and nutrients continue to enter the estuaries around the coasts there is potential for it to become a more common occurrence (Gao *et al.*, 2017). The difficulty of achieving nutrient reduction goals associated with point and nonpoint source removal, and rising implementation costs suggest that additional approaches of reducing nutrients in waterways could prove useful in the future (Higgins *et al.*, 2011). Understanding the mechanisms required to remediate the potential impact of increased nutrient loading on estuaries around the UK in the future would be of benefit.

Bivalve aquaculture is extractive, meaning that the deployment of mussels and other shellfish in the water reduces the concentration of particulate organic matter (Ferreira and Bricker, 2016). Nitrogen and phosphorus are taken up and used for both shell and tissue growth, and this is removed from the marine ecosystem when the animals are harvested (Carmichael *et al.*, 2012; Cerco and Noel, 2007). Paerl (2009) highlights that to effectively deal with eutrophication it is important to remove both N and P. Calculating the potential removal of nutrients through the harvest of bivalves is in theory relatively easy to measure and upscale to kg tonne⁻¹ of mussels. This is usually done based on literature values for tissue chemistry, but there is very little information on mussel tissue chemistry in the main areas of mussel production. It is possible to gather data on the total tonnages produced around the UK, combine this with nutrient analysis of the shell and tissue, and a total calculated (Timmermann *et al.*, 2019).

Variation in the tissue and shell nutrient concentrations will alter the amount of nutrient removal via harvested shellfish. These in turn are influenced by environmental factors such as food supply, temperature and seasonal spawning cycles (Hawkins and Bayne, 1985; Rodhouse et al., 1984; Rose et al., 2014; Smaal and Vonck, 1997). These environmental factors vary seasonally (Knopf et al., 2020). Typically, seasonal patterns in the condition of mussels are linked to spawning period, which typically occurs in spring and is followed by weight loss in summer; then a period of glycogen storage; followed by a period of gonad development in late autumn and winter (Gabbott, 1983). Studies have examined the differences in nutrients at different times of the year, but it has been highlighted that there is a lack of information on seasonal variation of nutrient content within sites (Rose et al., 2014). Some studies have presented some of the changes in tissues of mussels using C:N ratios. The C:N ratio of animal tissues provide a proxy of lipid to protein content and so can be informative of both lipid content and diet (Perkins et al., 2018). Sites with higher nutrient input are more susceptible to eutrophication (Nedwell et al., 2002), and as mussels are one of the proposed mechanisms to remove excess nutrients from the coastal environment, this study aimed to look at whether there were temporal differences in the C, N and P content of mussels from a high and low nutrient site. It is important to see if seasonal change varies between locations. Mcleod and Mcleod (2019) highlight the need for site-specific assessments to be carried out to gain sitespecific values for C, N and P removal, and this provides information for the potential, should mussels be used for nutrient remediation. Therefore, in this study, we aimed to test there were seasonal differences in C, N, and P percentage content in tissue and shell and test for differences in two nearby but contrasting sites. This study upscales this with the weight of mussels collected, to calculate the kg C, N, and P content per tonne of live mussels.

4.3 Methods

4.3.1 Site selection

To assess temporal variation in C, N and P contents of mussels, two sites were selected on the Menai Strait, North Wales, UK. Suitable sites were chosen based on CEFAS sanitary survey reports (Kershaw and Acornley, 2013a, 2013b), selecting estuaries where blue mussels (*M. edulis*) were present. Average concentrations of nitrate in the input rivers to each estuary were estimated from data in the harmonised river monitoring scheme (HRMS, available from <u>https://data.gov.uk/dataset/bda4e065-41e5-4b78-b405-41c1d3606225/historic-uk-water-</u>

quality-sampling-harmonised-monitoring-scheme-summary-data). The two sites chosen were the Afon Braint, a small river estuary in the south of the island. Its primary source is Llyn Llwydiarth, (coordinates: 53.283884, -4.178133), whose catchment contains mainly farmland, primarily fertilised pasture supporting livestock and estuary has an annual average nitrate concentration of 2.5 mg l⁻¹ and has wild mussels present. The second site chosen was the commercially managed mussel beds within the boundaries of the 1962 Menai Strait (east) Fishery Order. This site is more marine and has an annual average nitrate concentration of 0.06 mg l⁻¹. This site is the most important aquaculture site in Wales, and the biggest shellfish farming area in the UK. Both sites are intertidal, although the mussels at the Afon Braint are situated higher up the intertidal zone.

4.3.2 Sample collection

Preliminary analysis was conducted to assess between-individual and between-location variation. Preliminary analysis suggested that it was necessary to sample from five locations around each site and that six mussels were needed from each location to adequately account for within-site variation. Samples were collected monthly over 13 months, and mussels were chosen in the size range 40-90mm in length to represent mussel size at harvest.

4.3.3 Sample preparation

After collection, mussel shells were scraped clean of encrusting barnacles, patted dry using paper towels and the live weight was taken before the shell length was obtained using digital Vernier callipers. The mussels were placed in labelled zip lock bags before being frozen to - 18°C before analysis. In the laboratory, the mussels were defrosted, and the tissue completely removed from the shell. The wet weight of tissue was determined after gently rolling samples

in a paper towel to remove excess external water. Tissue samples were placed into tin dishes and frozen to -20°C before being placed in a freeze dryer for 120 h at a vacuumed temperature of -40°C. Once completely dry, the dry weight was taken. The mussels were hand-ground with a pestle and mortar and then placed into Precellys tubes with stainless steel ball bearings and ground to a fine powder. The tissue of the six mussels from each location was pooled and homogenised, creating five replicate samples to be analysed from each site. Shells from the pooled samples of six mussels were patted dry using paper towels and the wet weights taken, then oven-dried at 60°C for 120 h and dry weight taken. The dried shells were crushed with a hammer into small pieces, then placed in a hammer mill and ground to 1mm particles, and finally ground to a fine powder in a ball mill.

4.3.4 Condition Index

The condition index was used to represent seasonal variation in wet tissue content, whilst accounting for variability in the size of the mussel analysed using the following equation.

Condition index = Wet tissue weight $(g) / \text{length} (mm) \times 100$

4.3.5 Elemental analysis

Nutrient analysis was based around the methods of Higgins et al. (2011) and Zimmermann and Keefe (1997). N and C content was measured in subsamples of dried tissue and shell, using a Flash elemental analyser, with flash combustion (950°C) and measurement of gaseous products by gas chromatography. The dry weights of samples analysed were between 1 to 1.5 mg for tissue, and 9.5 to 10.5 mg for shell. Optimum sample weights were determined before analysis. All samples were run with carrier gas blanks, sample blanks (empty tin capsules), a duplicate sample, then acetanilide standards following every ten samples run. Each day samples were run Apple leaves NIST 1515 and NIES mussel tissue was run to ensure the machine-maintained accuracy. There was no observed drift in the calibration with time, and so elemental composition was calculated based on a mean for all blanks and acetanilide standards.

4.3.6 Phosphorus analysis

Phosphorus analysis was based on the methods of Solórzano and Sharp (1980). Mussel shell and tissue samples were weighed out into porcelain crucibles (100mg of tissue and 2g of shell), as well as samples of Certified Reference Material -BCR-684 (sediment). The samples, reference materials, and blanks were placed in a muffle furnace for 3 hours at 450°C. Once cooled, samples were placed in centrifuge tubes and acidified with 10 ml of 3.5 M HCl. If any sample remained in the crucible, they were rinsed with further aliquots of 3.5 M HCl and the

final volume made up to 20ml. These were placed on an orbital shaker for 16 hours, before centrifugation at 3000 rpm for at least 15 minutes or until all the supernatant was clear. 10 ml of the supernatant was pipetted into a 50 ml falcon tube.

To make a stock phosphate solution of 1000 mg per litre, 0.439 g of anhydrous KH_2PO_4 was dried overnight in an oven at 60°C. This was then dissolved in 100 ml of deionised water (DI water) and a range of standards from 0-100 ug l⁻¹ were used to create a calibration curve. Each standard had 10ml of 3.5 M HCl added, followed by 5 drops of Nitrocresol (4-Methyl-2-nitrophenol, C₇H₇NO₃, 0.25%). Each of the standards was then de-acidified with 9.5ml of 5M NaOH. If the solution did not change from a pale, clear yellow, then 0.5 ml of 5 M NaOH was added at a time until the solution darkened. The standards were then topped up to 50ml with DI water.

A colour developing reagent was made up with 50ml H_2SO_4 (2.5 M or 13 %), 5ml potassium antimony tartrate ($C_8H_{10}K_2O_{15}Sb_2$) solution (0.27 %), 15ml ammonium molybdate solution ((NH₄)₆Mo₇O₂₄) (10g in 100ml of DI water) and 30ml ascorbic acid ($C_6H_8O_6$) (1.76g in 100ml of DI water). 5 ml of each neutralised standard was pipetted into a clear plastic test tube, then 3 ml of DI water and 2 ml of colour developing reagent was added to each tube. These were allowed to stand for 15 minutes until the colour had developed and were analysed within one hour. The solution was then poured into 1.6 mm disposable UV cuvettes and measured using a spectrophotometer (Evolution 201). The 10 ml of the supernatant in the 50 ml falcon tube had 5 drops of Nitrocresol added. Each was then de-acidified with 9.5ml of 5M NaOH. If the solution did not change from a pale, clear yellow, then 0.5 ml of 5 M NaOH was added at a time until the solution darkened. The samples were then topped up to 50ml with DI water. 1ml of this sample solution was then pipetted into a clear plastic test tube, then 7ml of DI water and 2 ml of colour developing reagent was added to each tube. These also were allowed to stand for 15 minutes and analysed within one hour before being analysed with the spectrophotometer (Evolution 201 Spectrophotometer).

4.3.7 Upscaling

The individual mussel live weight, dry tissue weight, and dry shell weight were used to calculate the percentage of live weight made up of dry tissue and shell. The percentage C, N, and P can give different results to the kg of C, N, and P tonne⁻¹ of live mussels, due to variation in the proportion of tissue and shell in mussels around the UK. To find the mass of C, N and P tonne⁻¹ of live mussels, the percentage contents were upscaled to values of per tonne of live

mussels using the conversion factors derived from the live weight, wet weight and dry weight of each component (shell and tissue) measured during processing using the following formulae.

Dry Weight per tonne⁻¹ of mussels (kg) = $\frac{Average dry weight of animal (g)}{Average Live weight of animal (g)} \times 1000 \text{ kg}$

Dry Shell (kg) per tonne⁻¹ of mussels (kg) = $\frac{Average Shell dry weight (g)}{Average dry weight of animal (g)} \times Average dry weight (kg)$

Dry Tissue (kg) per tonne⁻¹ of mussels (kg) = Average dry weight of animal (kg) – Average Dry shell weight (kg)

4.3.8 Statistical analysis

General linear models were used to test whether measurements of C, N, and P in tissue and shell differed significantly between sites and months. The response variables were wet and dry tissue indices, dry shell index, C, N, and P percentage content, upscaled kg of C, N, and P per tonne of live mussels. To test for normality, The Shapiro–Wilk test was used to test for normality and Levene's test for homogeneity of variance in C, N and P content of mussels. These tests showed that data followed a normal distribution, so transformations were not performed. The explanatory variables were site and month, both were modelled as categorical variables and looked for potential interactions.

Backwards model was performed to identify significant variables (GLM, p \leq 0.05). This process involved removing terms from the full model and selecting the most parsimonious model with the lowest AIC score. Following this, an ANOVA F-test was carried out to test the significance of each variable in the final model. When interaction terms were significant at the $\alpha = 0.05$ level, the lsmeans package was used to conduct Tukey post hoc tests (Lenth, 2016). Post model validation was carried out using QQ plots and residuals vs fitted graphs (Zuur *et al.*, 2010). All analyses were constructed in R 3.5.0 (<www.r-project.org>, Studio 2012).

4.4 Results

4.4.1 Condition index

The condition index (Figure 9Figure 9) showed a general decline over the first five months sampled. From February to April there was a higher condition index at the Afon Braint than at the Menai Strait, but the decrease in condition index levelled out in April for the Menai Strait

(5.24), whilst it didn't stop decreasing until May for the Afon Braint (4.28). The Menai Strait condition index then increased more rapidly than the Afon Braint. The Menai Strait remained at a significantly higher condition index (effect of site) than the Afon Braint for the rest of the sampling period (GLM, p \leq 0.05).

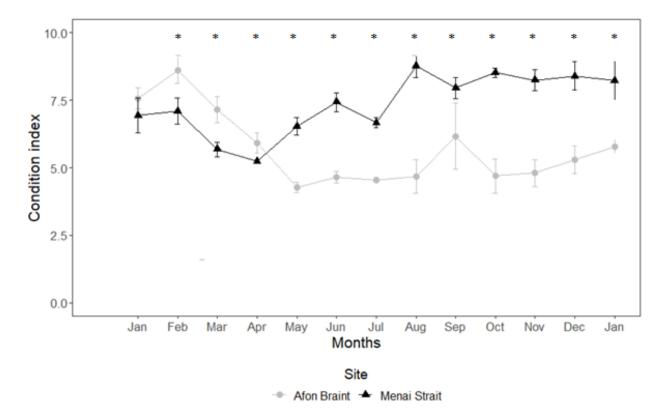


Figure 9 The condition index (with SE bars) for the Afon Braint (light grey line with circles and Menai Strait (black line with triangles), plotted against month. *represents significant difference for the GLM carried out on the condition index against month and the interaction of site, for the Afon Braint and Menai Strait, GLM analysis, $p \le 0.05$.

4.4.2 Tissue content

Typically, C, N, and P in tissue were highest in January, February, and March of 2018 before declining over the spring. The month that the minimum percentage content of C, N, and P was reached varied between sites before the percentage contents increased over the autumn and winter. The Afon Braint mussels had a C content in tissue of 44.2% before decreasing throughout the spring and summer to 39.4% in July (Figure 10Figure 10A). The Afon Braint mussels C content then increased throughout the autumn and winter reaching 43.4% by January 2019. Conversely, the mussels from the Menai Strait had a C content in tissue, reaching 38.3% C in

March, before increasing again to 42.5% by April. The percentage C content of mussels in the Menai Strait decreased slightly to 40.7% in September before increasing again in the winter, reaching a C content of 42.3%. Mussels from the Menai Strait had a significantly higher percentage C content than the Afon Braint (Effect of site, GLM, p \leq 0.05), although there was large variation throughout the year.

The percentage N content in tissue followed a similar pattern for both sites (Figure 10Figure 10B). Both had the highest percentage N content at the beginning of sampling (Afon Braint 9.7% N content and Menai Strait 9.6% N content), before decreasing between April and May. The Menai Strait percentage N content decreased to 5.9%, whilst the Afon Braint decreased to 7.6%. The percentage N content of mussels at both sites then increased throughout the summer and winter. By January of the next year the Afon Braint and Menai Strait mussel's percentage N contents were 10.2% and 9.8% respectively. Mussels from the Menai Strait had significantly lower percentage N content than mussels from the Afon Braint (Effect of site, GLM, p \leq 0.05).

The percentage P content in tissue followed the same pattern at both sites (Figure 10Figure 10C). The Menai Strait was had a slightly higher percentage P content than the Afon Braint in February and March. The peak percentage P content of tissue in mussels at the Menai Strait and Afon Braint was 2.4% and 2.1%, respectively. From this point onwards the percentage P at both sites then decreased to a minimum of 0.9% P content in July at the Menai Strait and 0.80% P content in August at the Afon Braint. After this, both sites then steadily increased for the rest of the sampling period. There was no significant difference in percentage P content in tissue between the two sites.

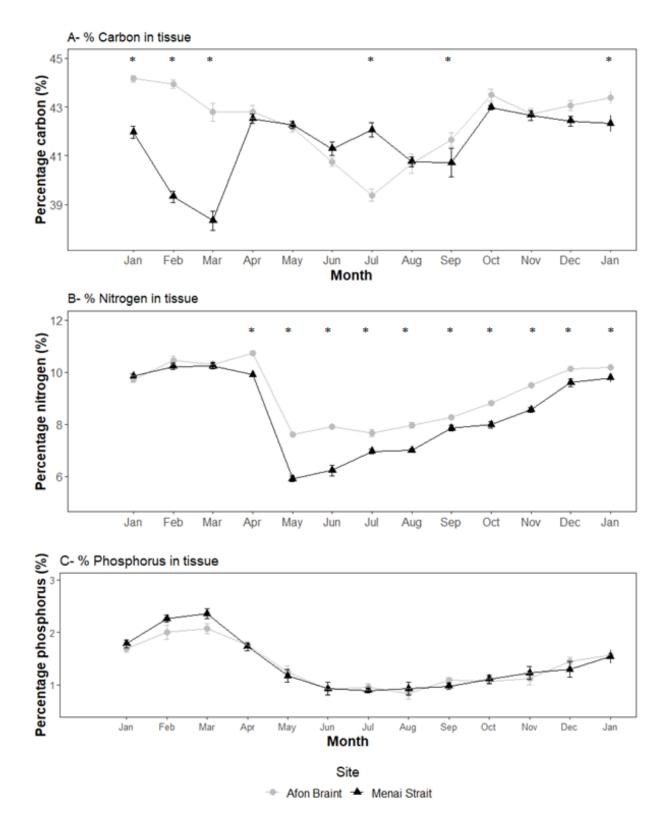
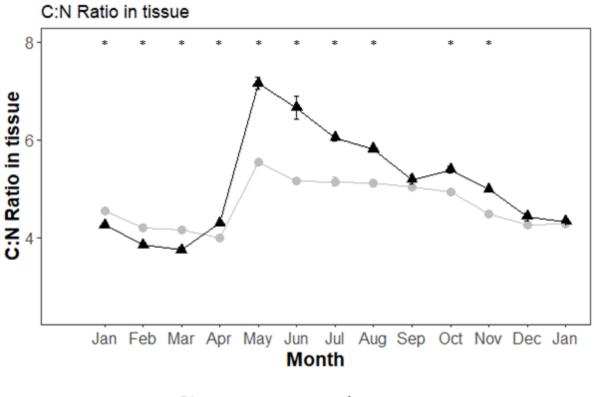


Figure 10 The carbon (A), nitrogen (B) and phosphorus (C) percentage content of tissue (with SE bars) for the Afon Braint and Menai Strait, plotted against month. *represents significant difference for the GLM carried out on the nutrient percentage content against month and the interaction of site, for the Afon Braint and Menai Strait, GLM analysis, $p \le 0.05$.

Using the percentage C and N content, CN ratio were calculated and plotted this against month (Figure 11). The Afon Braint had a C:N ratio of 4.54 in January 2018 and this decreased to 3.99 in April. It then increased significantly (Effect of month, GLM, p \leq 0.05) to a maximum of 5.54 in May, before decreasing steadily to 4.26 in January 2019. The Menai Strait followed a similar pattern to the Afon Braint and had a C:N ratio of 4.26 in January 2018 and this decreased to 3.75 in March. The CN ratio then increased significantly (Effect of site, GLM, p \leq 0.05) to a maximum of 7.16 in May, before decreasing steadily over the rest of the year to 4.33 in January 2019. Mussels from the Afon Braint had significantly different C:N ratio than mussels from the Menai Strait for all months except September, December, and January 2019 (Effect of interaction between month and site, GLM, p \leq 0.05).



Site 🖤 Afon Braint 📥 Menai Strait

Figure 11 The Carbon:Nitrogen (CN) tissue ratios in tissue (with SE bars) for the Afon Braint and Menai Strait, plotted against month. *represents significant difference for the GLM carried out on the C:N ratio in tissue against month and the interaction of site, for the Afon Braint and Menai Strait, GLM analysis, $p \le 0.05$.

4.4.3 Shell nutrient content

The Afon Braint mussels sampled in January 2018 had a C content in shell of 12.62%, and across the year only had a very small variation (Figure 12A). The mussels at the Afon Braint reached their maximum C content of 12.69% in May and a minimum of 12.37% in November, there was not however a significant difference between months. The Menai Strait followed the same pattern as the Afon Braint. Similarly, there was no significant variation between the different months. The Menai Strait mussels sampled in January had a C content in shell of 12.89% and reached their maximum C content of 13.03% in October and a minimum of 12.75% in July. The percentage C content in shell was significantly higher at the Menai Strait than at the Afon Braint (Effect of site, GLM, $p \le 0.05$).

The Afon Braint mussels sampled in January 2018 had a N content in shell of 0.35%, and across the year only had a very small variation (Figure 12B). The mussels at the Afon Braint reached their maximum C content of 0.38% in February and a minimum of 0.28% in December. There was a significant decrease in the percentage N content in shell between in November, December, and January 2019 (Effect of month, GLM, p \leq 0.05). The Menai Strait followed a similar pattern to the Afon Braint. However, there was no significant difference between months, although there was a 20% decrease in July and August. The Menai Strait mussels sampled in January had a C content in shell of 0.48% and reached their maximum N content of 0.54% in December and a minimum of 0.41% in July. The percentage N content in shell was significantly higher at the Menai Strait than at the Afon Braint (Effect of site, GLM, p \leq 0.05).

The Afon Braint mussels sampled in January 2018 had a P content in shell of 0.029% (Figure 12C). This then dropped to 0.017% in February and after this there was very little variation between months. The minimum P content was 0.014% in January 2019 and excluding January 2018, the maximum P content reached was 0.018% in November. The Menai Strait showed a very similar pattern to the Afon Braint. The Menai Strait mussels sampled in January 2018 had a P content in shell of 0.014%, and there was almost no variation across the year. The minimum P content was 0.011% in October and the maximum P content reached was 0.016% in August. There was a significant difference between the two sites in January 2018, October, and November.

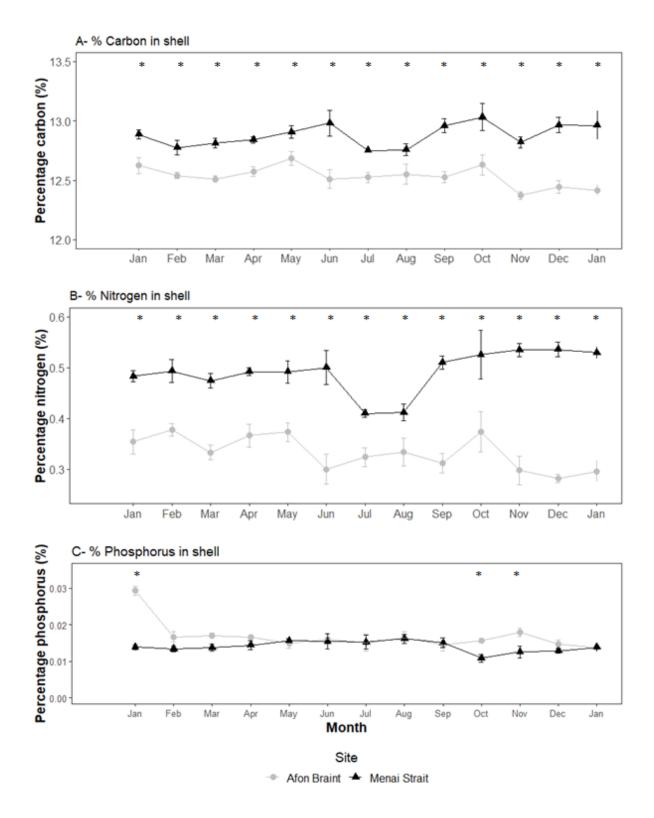


Figure 12 The carbon (A), nitrogen (B) and phosphorus (C) percentage content of shell (with SE bars) for the Afon Braint and Menai Strait, plotted against month. *represents significant difference for the GLM carried out on the kg of nutrient removed tonne⁻¹

against month and the interaction of site, for the Afon Braint and Menai Strait, GLM analysis, $p \le 0.05$.

4.4.4 Upscaling

Using the dry tissue and shell weights it was possible to upscale the kg of C, N, and P that would be produced per tonne of harvested live mussels in a nutrient remediation capacity (Appendix C - <u>Figure C 1</u>, <u>Figure C 2</u>, <u>Figure C 2</u>). This study presents values for C in shell, as this could be regarded as a long-term store of C, if not sequestration, and values for total N and total P removed from the system at harvest (Figure 13).

When upscaled the kg of C in shell per tonne of live mussels at the Afon Braint remained steady throughout the year (Figure 5A). There was very little variation and the minimum C per tonne of live mussels at the Afon Braint was 64.97 kg tonne⁻¹ and the maximum 68.11 kg tonne⁻¹. Conversely, the Menai Strait had a little more variation over the year. the minimum C per tonne of live mussels at the Menai Strait was 46.62 kg tonne⁻¹ in February and the maximum 55.50 kg tonne⁻¹ in July. The mussels at the Afon Braint had significantly more C in shell than those from the Menai Strait (Effect of site, GLM, p≤0.05).

When upscaled the kg tonne⁻¹ of N at the Afon Braint varied significantly with month (Effect of month, GLM, $p \le 0.05$). They increased from 5.37 kg tonne⁻¹ in January 2018 to 6.16 kg tonne⁻¹ in April (Figure 13B). The N then decreased to June reaching a minimum of 3.97 kg tonne⁻¹. N in mussels at the Afon Braint then increased again over the rest of the year, reaching 5.84 kg tonne⁻¹ in January 2019. Similarly, the Menai Strait varied significantly with month (Effect of month, GLM, $p \le 0.05$), increasing from 5.90 kg tonne⁻¹ in January 2018 to 7.35 kg tonne⁻¹ in April. The N then decreased to July reaching a minimum of 5.51 kg tonne⁻¹, before increasing again over the rest of the year, reaching 7.58 kg tonne⁻¹ in January 2019. There was a decrease between October (7.80 kg tonne⁻¹) and November (5.90 kg tonne⁻¹), but this had increased again in December (7.58 kg tonne⁻¹). Whilst there was some difference observed between the two sites, this was not found to be significant.

When upscaled the kg tonne⁻¹ of P at the Afon Braint varied significantly with month (Effect of month, GLM, p \leq 0.05). They increased from 0.76 kg tonne⁻¹ in January 2018 to 0.86 kg

tonne⁻¹ in March (Figure 13C). The N then decreased to August reaching a minimum of 0.36 kg tonne⁻¹. N in mussels at the Afon Braint then increased again over the rest of the year, reaching 0.73 kg tonne⁻¹ in January 2019. Similarly, the Menai Strait varied significantly with month, increasing from 0.79 kg tonne⁻¹ in January 2018 to 1.18 kg tonne⁻¹ in March (Effect of month, GLM, p≤0.05). The N then decreased to July reaching a minimum of 0.55 kg tonne⁻¹, before increasing again over the rest of the year, reaching 0.93 kg tonne⁻¹ in January 2019. Whilst there was some difference observed between the two sites, they were not found to be significantly different.

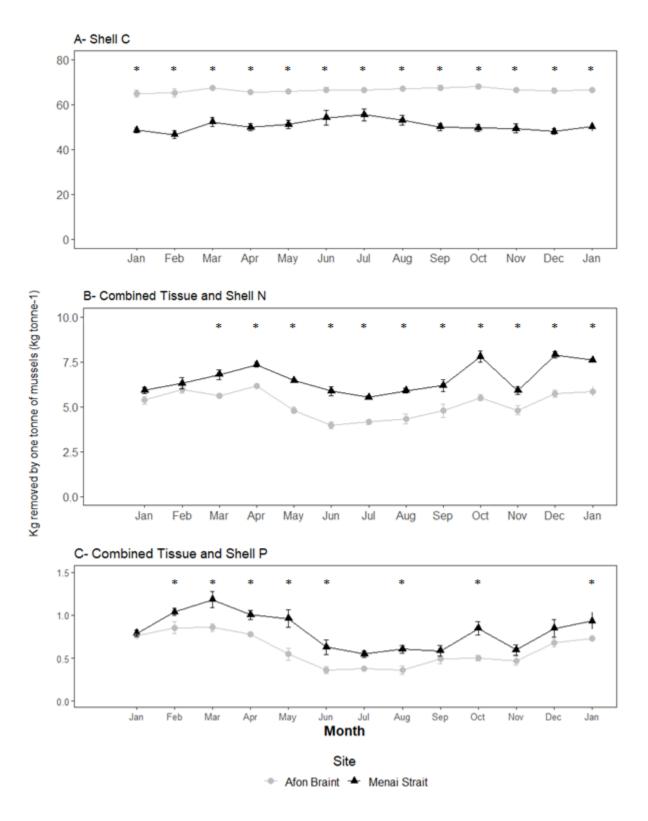


Figure 13 Upscaled carbon (A), nitrogen (B) and phosphorus (C) in tissue and shell (Kg tonne-1 live mussels removed) (with SE bars) for the Afon Braint and Menai Strait, plotted against month. *represents significant difference for the GLM carried out on the nutrient percentage content against month and the interaction of site, for the Afon Braint and Menai Strait, GLM analysis, $p \le 0.05$

When summarising the year to seasons of spring, summer and the winter (Table 14Table 14), the kg of N and P per tonne of mussels showed a cyclical pattern, starting high during the spring and falling to the start of the summer. This then increased over the winter to the end of the year. There was a 25% decrease between the peak N (kg tonne⁻¹) in the spring and the low in the summer. For P the decrease between the spring high and summer low was even greater, with a 50% drop in P (kg tonne⁻¹).

Table 14 Upscaled nitrogen (N) and phosphorus (P) (kg tonne⁻¹) for live mussel removed from the Afon Braint and Menai Strait Spring (January 2018-April), summer (May-August) and recovering during the winter (September-January 2019).

	N (kg tonne ⁻¹)		T-test	P-value	P (kg tor	nne ⁻¹)	T-test	P-value
	Afon	Menai			Afon	Menai		
	Braint	Strait			Braint	Strait		
Spring	$6.58 \pm$	5.77 ±	7.38	≤0.05	1.00 ±	0.81 ±	4.92	≤0.05
(Jan 2018-	0.17	0.10			0.04	0.02		
Apr)								
Summer	$5.93 \pm$	4.31 ±	3.71	≤0.05	0.68 ±	0.41 ±	3.41	≤0.05
(May-	0.11	0.12			0.05	0.03		
Aug)								
Winter	$7.07 \pm$	5.33 ±	8.85	≤0.05	0.76 ±	$0.57 \pm$	3.77	≤0.05
(Sep-Jan	0.20	0.14			0.04	0.03		
2019)								

4.5 Discussion

The seasonal changes observed in mussel condition index followed the pattern of the reproductive cycle (Gabbott, 1983). Shell presents less change than tissue, an obvious mechanism by which shell and tissue growth may be uncoupled is during periods of negative energy balance; soft tissues may decline in weight while shell cannot (Hilbish, 1986). The significant difference in N after April and P after March, was most likely due to changes in body composition following spawning. The C:N ratio of animal tissues provide a proxy of lipid to protein content and so can be informative of both lipid content and diet (Perkins et al., 2018) and this change is visible at both sites during this period. This is similar to the studies by Kautsky (1982) and Smaal and Vonck (1997) who identified, seasonal changes linked with gonad development and weigh loss of tissue. Borrero (1987) demonstrated that the length of

submersion and potential feeding time exert a profound influence on the timing of the reproductive cycle. More subtidal mussels can spawn rapidly in a single spawning event, whilst those that are more exposed to the air and cooler temperatures, higher up the shore have a longer trickle spawning event (Mangan et al., 2019; McQuaid and Phillips, 2006). This could explain the longer decrease in the percentage C content in tissue at the Afon Braint, comparatively to the mussels at the Menai Strait which had a sharp decrease over two months before quickly recovering. Mussels can be harvested all year, but harvesting usually stops during spawning and in the months immediately following it as the mussels condition is much lower (Pérez Camacho et al., 1991). Spawning took place at the two sites between April and May with the main spawning event at the Menai Strait occurring on the 22nd and 23rd of April (Demmer, 2020). High CN tissue ratios observed during summer in our study revealed that nitrogen content in tissue was low during late spring. Nitrogen content increased during late summer and autumn which coincides with the period of gonad dormancy following spawning. During this time glycogen storage and tissue growth takes place, with glycogen acting as an important and quickly mobilized source of stored glucose (Bayne et al., 1982). Seasonal fluctuations in tissue CN content observed in our study were comparable to those observed by Smaal and Vonck (1997) and Jansen et al. (2012), indicating that, following spawning, the mussels in this study increased their proportion of nitrogen to carbon ratio, as tissue growth increased.

The shells of the mussels at the Afon Braint were significantly heavier than mussels from the Menai Strait. Both sites are intertidal, although the Menai Strait site is submerged for longer periods due to the coastal morphology. It has been shown that mussels exposed at low tide more frequently are more vulnerable to predation and therefore develop thicker shells (Tagliarolo *et al.*, 2012). Of these two sites, the Afon Braint is a wild bed used for recreational collection, whilst the Menai Strait site is a commercial mussel bed and is managed. At the commercial bed, seed mussels are laid and grown at higher shore levels where they attain shell characteristics beneficial to predation resistance, before being re-laid lower down the shore, where they are submerged longer and achieve better growth due to increased food supply (Beadman *et al.*, 2003). The Afon Braint was the more exposed site, mussels there were unmanaged and were present there for their entire lives. The mussels there had heavier shells than the Menai Strait and this led to the Afon Braint removing significantly more C in shell. However, whether this is a form of carbon sequestration, remains uncertain due to a lack of

consensus within the literature (Filgueira *et al.*, 2015; Hickey, 2009; Tang *et al.*, 2011; Waldbusser *et al.*, 2013).

The significant negative relationship between P in shell and salinity recorded in chapter 3 suggests that the ability to remove P through shell production will be more efficient in systems with lower salinity. The Afon Braint site had a larger input of fresh water, which could explain the higher level of P in shell. However, when the total P in shell and tissue was combined, the Menai Strait mussels had more kg of P tonne⁻¹. This is likely to be due to mussels from this site were more subtidal, and therefore putting less effort into shell production. Coupled with this, other studies have found reduced growth with decreasing salinity and, therefore, mussels in lower salinity environments will generally be smaller (Riisgård *et al.*, 2012). This indicates, that while nutrient loading was higher at the Afon Braint site, other environmental factors, such as level of exposure, and freshwater input had more of an effect on the mussels.

In terms of potentially using the mussels at either of these sites to remove nutrients, our results show that the time of year had significant effects on the amount of N and P removed in harvested mussels. Most of the removed N and P was held with the tissues, with a small amount in shell. Mussel farmers harvest based on market demand but avoid harvesting following spawning events as there is a reduced meat condition (Pérez Camacho *et al.*, 1991). The results show that if mussels were to be used for nutrient remediation, the most effective time to harvest them to remove the most N and P from the system would be directly before spawning or once the mussels had recovered following spawning (April to December). This followed a similar trend at both sites, but there was significantly higher percentage content of N at the Afon Braint. The implication of this on nutrient remediation schemes using bivalves, is that the seasonal variation is an important factor to consider when deciding when to harvest. If harvested in the spring before spawning takes place, it is possible to remove 25% more N and 50% more P.

Many proposed nutrient remediation schemes using bivalves have suggested oyster reefs as a potential species suitable for remediation in high nutrient intertidal areas (Clements and Comeau, 2019; Higgins *et al.*, 2011; Reitsma *et al.*, 2017). These studies have however not accounted for temporal variation in their removal potential, which can now be highlighted as an important factor. This study has found that mussels, which are situated more subtidally have greater potential as nutrient remediators than intertidal mussels higher up the shore. This would indicate that further work could be carried out to assess the comparative cost-effectiveness of nutrient removal from constantly submerged rope cultured mussels compared to intertidal or

subtidal benthic farms. Rose *et al.* (2015) also highlight that in busy coastal environments, spatial constraints will be an important limiting factor , so that rope based systems may represent both more effective use of marine space for nutrient remediation and potential for siting in a wider range of water depths.

4.6 References

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5 The potential of mussel aquaculture in the UK – Scenariobased valuations of ecosystem services provided by blue mussels, *Mytilus edulis*.

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This paper has not been published, but is in preparation for publication. The PhD candidate carried out all work, analysis and writing.

5.1 Abstract

In the context of a declining mussel production within the UK, this study looks at a range of future options for a continued decline or an increase and expansion of the UK mussel industry by taking an ecosystem services approach. Utilising the kg of carbon, nitrogen and phosphorus tonne⁻¹ results from the UK spatial survey, it was possible to carry out an economic analysis of four different scenarios. Retaining mussel aquaculture at current levels (Status quo); further decline to approximately 20% of current production due to trade restrictions with the European Union (Trade Failure); increase of bottom culture to levels of 2012 through seeding from spat collection (Recovery); and doubling mussel aquaculture from 2012 levels with offshore mussel farms (Expansion). Currently non-food ecosystem services provide the equivalent of US\$20.3 million year⁻¹ in nutrient remediation and shell, however, should there be a trade failure nonfood ecosystem services could decrease to a value of only US\$4.1 million year⁻¹. With intervention, such as the restocking using spat collectors, bottom aquaculture can be restored to the levels of 2012, increasing the value of the associated ecosystem services to potentially be worth US\$37.4 million year⁻¹. It is possible to go further still and expand to offshore aquaculture, increasing the value of non-food ecosystem services to as much as US\$73.7 million year⁻¹. Defra estimated in 2019 that in England, businesses, the third sector, and public sector jointly spent approximately US\$3.45 billion a year to protect the water environment through water treatment, mitigation and restoration. Whilst not the solution, mussel aquaculture is already contributing but could make a more substantial contribution towards nitrogen and phosphorus reduction through the direct removal of these nutrients from coastal waters as well as providing usable products in shell and meat.

Keywords: Ecosystem services · Economic valuation, Nutrient Remediation, Shellfish Aquaculture

5.2 Introduction

Half of all aquaculture production is made up of lower trophic species, including shellfish and algae, (Science Advice for Policy by European Academies, 2017). Bivalves (primarily clams, mussels and oysters) accounted for 16 million tonnes of coastal and marine animal aquaculture in 2015, with an estimated market value of \$17.1 billion (FAO 2016) and in the UK the farming of mussels is the largest shellfish aquaculture sector by volume. Over the last decade, there has been a growing interest in the ecosystem services provided by shellfish aquaculture, and the ecosystem services benefits they provide in coastal waters. Historically dominated by provisioning services, the focus began on constraints to production and the possibilities for expansion (Gentry *et al.*, 2017). In more recent times, focus has moved on to other regulating and cultural services (Carrs *et al.*, 2020; Lacson *et al.*, 2019; Van der Biest *et al.*, 2020; van der Schatte Olivier *et al.*, 2018).

Regulating services, such as nutrient remediation, have become one of the largest areas of interest of bivalve aquaculture for researchers and producers. In recent years mussel farms have been discussed as a tool to be placed in estuaries and reduce the impact of terrestrial nutrient inputs through their ability to filter phytoplankton and incorporate carbon (C), nitrogen (N) and phosphorus (P) into their shells and tissue (Clements and Comeau, 2019; Petersen et al., 2019; Rose et al., 2015). The transport of P from terrestrial to oceanic environments can have implications for the quality of fresh and marine waters and has been shown to increase chlorophyll concentrations (Eyre and Balls, 1999), and P is regarded as a key element contributing to eutrophication as well as algal and planktonic blooms (Davidson et al., 2014). Historically, P was regarded as the priority nutrient controlling upstream freshwater productivity, whilst N was the limiting factor in coastal waters, however, changing anthropogenic activities have caused imbalances in N and P loading, making it difficult to control eutrophication by reducing only one nutrient (Paerl, 2009). There is relative consensus on the opportunities for the use of bivalves as nutrient remediators ((Ferreira and Bricker, 2018; Timmermann et al., 2019)). However, with respect to C sequestration, much debate remains. It was found that in the UK bottom cultured mussel shells contained 60.15 ± 0.77 kg C tonne⁻¹ and rope cultured mussel shells contained $46.12 \pm 1.69 \text{ kg C}$ tonne⁻¹ (**Chapter 3**). Despite this, currently it is not considered as a form of sequestration due to the CO_2 released during calcification and respiration (Filgueira *et al.*, 2015) and so is not included in this study.

Much of the extra value to non-food based ecosystem services has been found to be in the potential use of shell as aggregate (US\$ $0.3-0.9 \text{ kg}^{-1}$,(Morris *et al.*, 2018; van der Schatte Olivier *et al.*, 2018)), or for other purposes. Mussel shells (*Mytilus galloprovincialis*) have been used as a soil liming agent in agriculture in Galicia, Northern Spain (Garrido-Rodríguez *et al.*, 2013; Morris *et al.*, 2018; Osorio-López *et al.*, 2014). However, more recently, there has been discussion about the use of mussel shell in aggregate mixes (Morris *et al.*, 2018), mussel shell waste as a replacement for graded sands in the sand filter (Craggs *et al.*, 2010) and incorporation of crushed mussel shell waste in Spain into building mortars (Ballester *et al.*, 2007).

Cultural services are also provided by bivalves, with many examples of imagery and references to shells in cultures throughout the world (Carrs *et al.*, 2020; Duncan and Ghys, 2019; van der Schatte Olivier *et al.*, 2018). However, cultural services remain a challenge to quantify and assess (Chan *et al.*, 2012), and research on cultural services remains a small proportion of that undertaken for the other ecosystem services (Fish *et al.*, 2016; García Rodrígues *et al.*, 2017).

In recent years, the UK, has experienced a decline in mussel production (Ellis *et al.*, 2015). Possible reasons for this decline include poor shellfish spat fall and changes in the timing of the spat fall in recent years (Adamson *et al.*, 2017). The majority of spat used in mussel aquaculture is wild-caught, either caught in the water column as larvae settling on specialised spat catching ropes or harvested directly from a range of settlement substrata, such as macroalgae or from among adult mussel beds (Skelton and Jeffs, 2020). However, supplies of wild-caught spat are often irregular and unpredictable, making mussel aquaculture difficult to manage. In recent years, there has been a loss of spat due to predation, and furthermore, the harvesting of wild-caught spat is increasingly being brought under catch controls, which can further limit production (Alfaro *et al.*, 2010; Skelton and Jeffs, 2020; Walter and Liebezeit, 2003).

In England, Wales and Northern Ireland, the majority of mussels are produced through bottomculture, however, rope-grown mussels are produced in several locations (Hambrey and Evans, 2016). By contrast, Scotland's mussel industry is entirely composed of rope or suspended aquaculture (Chamberlain, 2002). In Scotland, concerns about variation in wild spat fall have led to the establishment of a pilot-scale blue mussel hatchery in the Shetland Islands in order to ensure the provision of spat, allowing the Scottish industry to reduce its reliance on wild resources (Adamson *et al.*, 2017). Another option now being looked at by the industry would be to utilise spat collectors, collecting larvae from the water column, which naturally attach themselves to ropes. Mussel growers in the south of the UK are currently using this method and experiencing high rates of wild mussel settlement (Suplicy, 2018; van den Burg *et al.*, 2017). Therefore, this could provide a system with which to supply the seed mussel requirements of the bottom culture industry.

Since 2016 the UK mussel industry has been under additional pressures following the forthcoming exit of the UK from the European Union, potentially losing access to the European markets. Delays are anticipated to occur post-exit of the European Union as a result of additional paperwork and physical checks at borders and additional time/cost prior to dispatch. The shellfish sector, including aquaculture production of mussels, is very heavily dependent on high-end export markets which account for around 80% of total production (Symes and Phillipson, 2019). The principal market for UK mussels is the Netherlands, which accounts for 98% of UK mussel exports to the EU. In the absence of a free trade agreement, the EU applies the most favoured nation (MFN) tariffs, which would mean a 10% tariff (Cumulus Consultants, 2018). The potential loss of this market until trade deals are in place could impact on mussel farming businesses and the level of production.

Within the UK, both the Welsh government (2013) and Scottish government (Scotland Food & Drink, 2016) have stated their intention to double the economic income of the aquaculture industry, and it could be assumed that the rest of the UK would aim to follow the same goal and increase their aquaculture production. An industry-led sustainable growth of the aquaculture industry would align with goals set out by the Food and Agriculture Organization of the United Nations (FAO, 2016). Limitations on, and competition for, inshore water space is making offshore shellfish developments the logical method for expansion (Stevens *et al.*, 2008). Recently this has become a popular option, with mussel culture in high-energy, open ocean environments on submerged long-lines in the middle of the water column (Mizuta *et al.*, 2019).

In **chapter 3** of this thesis, the spatial survey of the UK provides data to investigate the potential of shellfish farming as a method of coastal nutrient remediation. This includes a wide range of environmental and physical conditions including nutrient loading in catchments, sea surface temperatures, salinity, and culture method. Previous estimates of nutrient remediation by

shellfish have used literature values for tissue nutrient composition and applied this to data from many different environmental settings (e.g. (van der Schatte Olivier *et al.*, 2018). The findings of **chapter 3** allow for estimation UK-wide specific values of N and P removal to be used, with separation of benthic and suspended culture systems. The results allow the calculation of the tonnage of shell that is produced in the UK, and that, therefore, could be utilised as aggregate.

The aim of this study was to explore the potential effect of four scenarios on the mussel production and associated ecosystem services of the UK mussel aquaculture industry: - *Status quo*, Trade failure, Recovery, and Expansion. The study will compare these scenarios by applying economic valuations to the services where possible.

5.3 Methods

This study presents the decline in the UK mussel aquaculture industry and examines four scenarios for mussel production in the UK. These were considered to forecast several possible scenarios for the amount of ecosystem services of mussel aquaculture (e.g. *status quo*, trade failure, recovery and expansion) and for financial market returns (in cash or subsidies) in each of those scenarios.

Scenario 1 – Status quo

This scenario makes the assumption that the UK will retain mussel aquaculture at current levels, and suppose that due to external factors, such as predation and loss of seed, that production is unable to recover to the levels of 2012 and remains at the level of 2018.

Scenario 2 – Trade failure

This scenario makes the assumption that there is an 80% reduction (the current level of export to the European union) of mussel harvest from the levels of 2018 production, due to the loss of European markets, although could represent other large decreases in mussel production.

Scenario 3 – Recovery

This scenario makes the assumption that harvest returns to 2012 levels of production (with Scotland maintaining the level it had reached in 2018, as this was higher than the level of

production in 2012). Due to improvements in seed supply through hatcheries, the use of spat collectors, and natural settlement, allowing for, the restoration of mussel beds. This would also assume the maintenance of current market access.

Scenario 4 – **Expansion**

This scenario makes the assumption that the tonnages of 2012 are doubled, as proposed as the aspirations of the Welsh and Scottish governments, in all four countries of the United Kingdom. The expanded aquaculture will be assumed to done through offshore rope sites, at each of the four countries (England, Wales, Scotland and Northern Ireland).

5.3.1 Economic analysis

The economic analysis of this study aims to value a range of ecosystem services carried out by the UK mussel aquaculture industry. The calculations carried out are based on the levels of production, combined with the levels of service per tonne of production and the economic values of the services. The following sections address the components of this.

5.3.1.1 Production and value of food ecosystem services

Mussel tonnage data in England, Wales, Scotland and Northern Ireland between 2012 and 2018 were gathered from Eurostat (https://ec.europa.eu/eurostat/data/database), FAO websites (http://www.fao.org/fishery/statistics/software/fishstatj/en), Scottish government website (https://www2.gov.scot/Topics/marine/Publications/stats/ShellfishProduction2009)

and marine Scotland (<u>https://data.marine.gov.scot/group/aquaculture</u>). This also provided the value of mussels in each of the four countries over this time. These data were used to carry out an economic valuation of ecosystem services provided by the blue mussel, *Mytilus edulis* under the various scenarios, by multiplying the tonnage with the market price.

5.3.1.2 Nitrogen, and phosphorus data

The tonnages were combined with results from **chapter 3** (summarised in <u>Table 15Table 15</u>) to calculate the tons of total N and total P in *M. edulis*. The percentage of C, N, and P were upscaled to values per tonne of live mussels using the conversion factors derived from the live weight, wet weight and dry weight of each component (shell and tissue) measured during processing. **Chapter 3**, found that there were significant differences between rope and bottom cultured mussels, therefore, averaged values for each culture method were used in the economic

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scenarios. Additionally, P in tissue had a significant negative relationship with mean annual seawater temperature for both rope and bottom cultured sites. Similarly, the percentage content of phosphorus in shell had a significant negative relationship with increasing salinity. However, the tonnages of mussels produced in the UK only gave a total value for each country, and so it was not possible to include these site-specific relationships in the UK calculation. Due to this lack of spatial information, it was therefore necessary to use an average of the N and P data collected around the UK and therefore it was not possible to calculate the statistical confidence or variation.

Table 15 Percentage of total mussel that is shell, Kg of carbon in shell per tonne of live animal (Chapter 3).

	Rope cultured mussels	Bottom cultured mussels
Percentage of total mussel that is	35.3%	48.7%
shell		
Kg N tonne ⁻¹ live weight	8.5	5.0
Kg P tonne ⁻¹ live weight	0.950	0.430

5.3.1.3 Economics

The economic value of N removal (Beseres Pollack *et al.*, 2013; Newell *et al.*, 2005), P removal (Molinos-Senante *et al.*, 2011) and using whole or crushed shells as aggregate (Morris *et al.*, 2018) were taken from literature and are summarised in <u>Table 16Table 16</u>. These values assume the source prices from the literature, although these could potentially vary. In order to account for this, the range of potential value was calculated, along with the mean. All values used in the four scenarios were converted to the effective value in 2018, to compare the ecosystem service gains and losses. This was carried out by converting the values using purchasing power parity (PPP) exchange rates before they were adjusted to real 2018 values using the appropriate national GDP deflators. The values were then converted to International \$ (2018) using the relevant purchasing power parity exchange rate.

Table 16 Valuation for 1kg of nitrogen removal, P removal and shell aggregate after conversion values adjusted to 2018 prices, using PPP exchange rates. Italicised values are mean value calculated from the literature.

Value	US\$ kg ⁻¹	Method of valuation	Source
Phosphorus	11.7	Value based on the negative environmental impact	Molinos-Senante et al.
minimum		on the receiving area, and with this value the	(2011)
Phosphorus	52.4	removal of P based on the environmental benefit	
maximum		derived from the recovery of the nutrient.	
Phosphorus average	32.1	_	
Nitrogen minimum	9.1	Replacement cost approach to assess the cost	Beseres Pollack et al.
		equivalent value of the nutrient regulating service	(2013)
		that bivalves provide,	
Nitrogen maximum	30.4	Sum of all commercial and non-commercial	Newell <i>et al.</i> (2005)
		benefits generated, by its impact on water quality	
Nitrogen average	20.5		
Shell minimum	0.2	Value of use as shell aggregate	Morris et al. (2018)
Shell maximum	0.7	-	
Shell average	0.6	-	

5.4 Results

5.4.1 Tonnages produced

The decline in bottom mussel culture in the UK is shown in Figure 14Figure 14. In 2012, England was producing 6,000 tonnes of mussels, but saw a sharp decline between 2012 and 2014, decreasing to 1,500 tonnes, before levelling off and maintaining production of between 1,000-2,000 tons year⁻¹. Wales, meanwhile, experienced a gradual decline in production from 2012 until 2015, reducing from 9,000 tonnes down to 7,000 tonnes. Following this, however, there was a sharp decrease to 1,500 tonnes in 2017. Northern Ireland has generally experienced a steady decrease, initially producing 4,800 tonnes in 2012, to the present where production is 2,000 tonnes. Northern Ireland did show an increase in 2017, where it produced nearly 5,000 tonnes, but this appears to be an anomaly within the trend. Conversely, Scotland has steadily increased its production from 2012, where it produced approximately, 6,300 tonnes, to 2017, where there was a Scottish production of 8,200 tonnes. In 2018, however, this had decreased slightly, down to 6,900 tonnes.

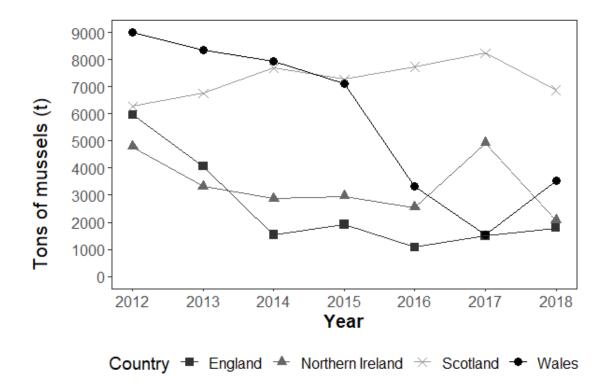


Figure 14 UK production of mussels (t) between 2012 and 2018.

5.4.2 Effect of scenarios on tonnage

When the four scenarios were applied to mussel production in the UK (Figure 15), they had a noticeable effect on the tonnages produced by each of the four countries. Scenario 1 represented the situation at present, with Scotland producing almost half of all mussels through rope cultured mussels (6,874 tonnes), whilst the rest of the UK combined, produced 7,194 tonnes. When scenario 2 was applied to mussel production, it showed a large decrease in tonnage for all culture methods in the four countries, with the entire UK total producing 2,850 tonnes. Scenario 3 saw the increase of bottom cultured mussels to the levels of 2012, with Scotland maintaining the level it had reached in 2018 This led to a total production of 26,618 tonnes of mussels being produced. Scenario 4 showed that by expanding from this through offshore rope aquaculture, 52,042 tonnes could be produced.

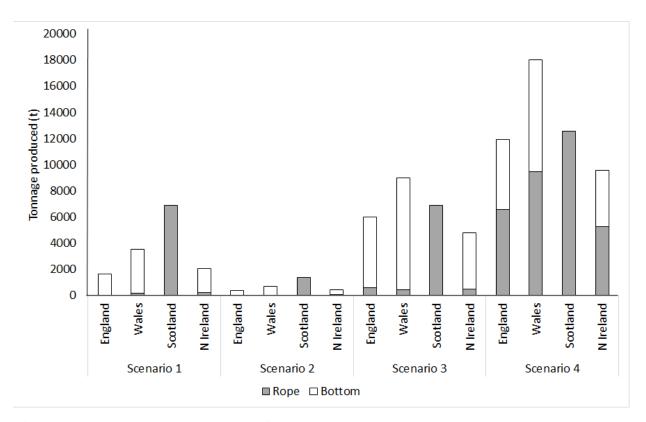


Figure 15 Total annual tonnage of mussels produced in rope and bottom mussel aquaculture in the UK under four scenarios (Scenario 1 – Status quo (Rope = 7,256 t, Bottom = 6,812 t, Total = 14,068 t), Scenario 2 – Trade failure (Rope = 1,487 t, Bottom = 1,363 t, Total = 2,850 t), Scenario 3 – Recovery (Rope = 8,399 t, Bottom = 18,219 t, Total = 26,618 t), and Scenario 4 – Expansion (Rope = 33,823 t, Bottom = 18,219 t, Total = 52,042 t)).

5.4.3 Nitrogen removal

The kilograms of N removed, and subsequent monetary valuations are shown in <u>Table 17</u>Table 17. Using the average nitrogen value (US\$20.5 kg⁻¹, <u>Table 16</u>Table 16), scenario 1 represents the N currently being removed around the UK at harvest, which amounts to 121 tons year⁻¹ worth an estimated US\$16.5 million year⁻¹. Scenario 2 shows the potential effect that leaving the European Union without a trade deal could incur on N removal. This would reduce N removal to 24 tons year⁻¹ (US\$3.3 million year⁻¹). In contrast, scenario 3 shows that by restoring commercial mussel beds to the levels they were in 2012, the N removed would be almost doubled to 221 tons year⁻¹, increasing the value of N removal to US\$30.2 million year⁻¹. Finally, in scenario 4, if the UK met the targets set by Wales and Scotland, to double aquaculture, then mussels would be able to remove 442 tons of N worth an estimated US\$60.3 million year⁻¹.

Table 17 Kg of nitrogen removed and value in US\$ converted to 2018 PPP values, under four scenarios (Scenario 1 – Status quo, Scenario 2 – Trade failure, Scenario 3 – Recovery, and Scenario 4 – Expansion). Bracketed values account for the range of valuations available through literature for the different services.

		Nitrogen re	moved (kg)			Value (US\$ 000)			
		Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 1	Scenario 2	Scenario 3	Scenario 4
England	Rope	1,520	300	5,070	55,780	207 (16- 398)	41 (3- 79)	691 (56- 1,326)	7,604 (621- 14,587)
	Bottom	13,720	2,740	45,640	45,640	1,870 (152- 3,587)	374 (30- 717)	6,222 (508- 11,935)	6,222 (508- 11,935)
	Total	15,240	3,050	50,710	101,420	2,077 (169- 3,985)	415 (33- 797)	6,913 (565- 13,261)	13,826 (1,130- 26,523)
Wales	Rope	1,500	300	3,820	80,290	203 (16- 391)	40 (3- 78)	521 (42-999)	10,946 (894- 20,997)
	Bottom	28,420	5,680	72,640	72,640	3875 (316- 7,433)	775 (63- 1,486)	9,903 (809- 18,997)	9,903 (809- 18,997)
	Total	29,920	5,980	76,470	152,930	4,079 (333-7,824)	815 (66- 1,564)	10,425 (852- 19,997)	20,850 (1,704- 39,995)
Scotland	Rope	58,430	11,690	58,430	106,710	7,965 (651- 15,280)	1,593 (130- 3,056)	7,965 (651- 15,280)	14,548 (1,189- 27,907)
	Bottom	0	0	0	0	0	0	0	0
	Total	58,430	11,690	53,350	106,710	7,965 (651- 15,280)	1593 (130- 3,056)	7,965 (651- 15,280)	14,548 (1,189- 27,907)
Northern	Rope	1,750	350	4,070	44,720	238 (19- 457)	47 (3-91)	554 (45- 1,063)	6,096 (498- 11,694)
Ireland									
	Bottom	15,760	3,150	36,590	36,590	2,148 (175- 4,121)	429 (35- 824)	4,988 (407- 9,568)	4,988 (407- 9,568)
	Total	17,510	3,500	40,650	81,300	2,387 (195- 4,579)	477 (39- 915)	5,542 (453- 10,631)	11,084 (906- 21,263)
UK	Rope	63,200	12,640	71,390	287,490	8,616 (704- 16,528)	1,723 (140- 3,305)	9,732 (795-18,669)	39,195 (3,204- 75,187)
	Bottom	57,900	11,580	154,870	154,870	7,893 (645- 15,142)	1,578 (129- 3,028)	21,113 (1,725- 40,501)	21,113 (1,725- 40,501)
	Total	121,100	24,220	226,260	442,360	16,510 (1,349- 31,670)	3,302 (269- 6,334)	30,846 (2,521- 59,171)	60,309 (4,929- 115,689

5.4.4 Phosphorus removal

In comparison with N, mussels remove relatively small quantities of P (<u>Table 18</u>Table 18). Using the average phosphorus value (US\$32.1 kg⁻¹, <u>Table 16</u>Table 16), at present, scenario 1 shows that mussels in the UK are removing 10 tons of P year⁻¹, worth an estimated US\$320,000 year⁻¹. If the UK were to lose access to European markets, and mussel aquaculture was to decrease, then 2 tons of P would be removed per year, worth US\$64,000. If, however, mussel aquaculture was restored to the levels of 2012 (scenario 3) this would increase P removal by around 50% to 15.8 tons P year⁻¹, worth an estimated US\$507,000. If mussel aquaculture was to be expanded further through rope systems (scenario 4), this would more than double P removal to 40 tons, worth an estimated 1.3 million year⁻¹.

5.4.5 Shell production for aggregate

Currently, the UK produces around 5,941 tons of shells in the mussel industry, which at present are largely seen to have no value (<u>Table 19</u><u>Table 19</u>). Often these are thrown away as a waste product of the food industry. Mussel shell is sold to decorate gardens, but this does not happen for most of the shells produced in the UK mussel aquaculture industry. Using the average value of shell as aggregate (US\$0.6 kg⁻¹, <u>Table 16</u><u>Table 16</u>), it is estimated that the value of this shell as an aggregate could be worth US\$3.5 million year⁻¹ at present (Scenario 1). Similarly, to the other services calculated should the UK lose access to the European markets (Scenario 2), 1,188 tonnes of shell would be produced year⁻¹, worth US\$691,000 year⁻¹. The potential value of shell as aggregate would increases should bottom aquaculture return to the levels of 2012 (scenario 3) producing 11,832 tonnes of shell worth US\$6.9 million. Should an expansion of mussel aquaculture take place (scenario 4), and targets to double production are met through rope production, this would produce 20,812 tons of shell worth US\$12.1 million year⁻¹.

Table 18 Kg of phosphorus removed and value in US\$ converted to 2018 PPP values, under four scenarios (Scenario 1 – Status quo, Scenario 2 – Trade failure, Scenario 3 – Recovery, and Scenario 4 – Expansion). Bracketed values account for the range of valuations available through literature for the different services.

		Phosphorus	removed (kg	;)		Value (US\$ 000)				
		Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 1	Scenario 2	Scenario 3	Scenario 4	
England	Rope	170	30	570	6,230	5 (2- 8)	1 (0- 1)	18 (6- 29)	200 (73- 326)	
	Bottom	690	140	2,310	2,310	22 (8- 36)	4 (1- 7)	74 (27- 121)	74 (27- 121)	
	Total	860	170	2,880	8,540	27 (10- 45)	5 (2-9)	92 (33- 150)	274 (100- 447)	
Wales	Rope	170	30	430	8,970	5 (1-8)	1 (0- 1)	13 (5- 22)	287 (105- 470)	
	Bottom	1,440	290	3,670	3,670	46 (16- 75)	9 (3- 15)	117 (43- 192)	117 (43- 192)	
	Total	1,610	320	4,100	12,650	51 (18- 84)	10 (3- 16)	131 (48- 215)	405 (148- 663)	
Scotland	Rope	6,530	1,310	6,530	11,930	209 (76- 342)	41 (15- 68)	209 (76- 342)	382 (140- 625)	
	Bottom	0	0	0	0	0	0	0 (0- 0)	0	
	Total	6,530	1,310	6,530	11,930	209 (76- 342)	41 (15-68)	209 (76- 342)	382 (140- 625)	
Northern Ireland	Rope	200	40	450	5,000	6 (2- 10)	1 (0- 2)	14 (5-23)	160 (58- 262)	
	Bottom	800	160	1,850	1,850	25 (9- 41)	5 (1- 8)	59 (21- 97)	59 (21- 97)	
	Total	990	200	2,310	6,850	31 (11- 52)	6 (2- 10)	73 (27- 120)	219 (80- 359)	
UK	Rope	7,060	1,410	7,980	32,130	226 (82- 370)	45 (16-74)	256 (93- 418)	1,030 (377- 1,684)	
	Bottom	2,930	590	7,830	7,830	93 (34- 153)	18 (6- 30)	251 (92- 410)	251 (92-410)	
	Total	9,990	2,000	15,810	39,970	320 (117- 523)	64 (23- 104)	507 (185- 829)	1,282 (469- 2,095)	

Table 19 Tonnes of shell removed for aggregate and value in US\$ converted to 2018 PPP values, under four scenarios (Scenario 1 – Status quo, Scenario 2 – Trade failure, Scenario 3 – Recovery, and Scenario 4 – Expansion). Bracketed values account for the range of valuations available through literature for the different services.

	Bottom	785	157	2,612	2,612	456 (185- 555)	91 (37- 111)	1,520 (615- 1,846)	1,520 (615- 1,846)
	Total	849	170	2,823	4,930	493 (199- 599)	98 (39- 119)	1,642 (665- 1,995)	2,869 (1,161- 3,485)
Wales	Rope	62	12	159	3,336	36 (14- 43)	7 (2-8)	92 (37- 112)	1,941 (786- 2,358)
	Bottom	1,627	325	4,158	4,158	946 (383- 1,150)	189 (76- 230)	2,419 (979- 2,939)	2,419 (979- 2,939)
	Total	1,689	338	4,317	7,495	982 (398- 1,194)	196 (79- 238)	2512 (1,017- 3,051)	4,361 (1,765- 5,297)
Scotland	Rope	2,428	486	2,428	4,434	1,412 (572- 1,716)	282 (114- 343)	1,412 (572- 1,716)	2,580 (1,044- 3,134)
	Bottom	0	0	0	0	0 (0- 0)	0 (0- 0)	0 (0- 0)	0
	Total	2,428	486	2,428	4,434	1,412 (572- 1,716)	282 (114- 343)	1,412 (572- 1,716)	2,580 (1,044- 3,134)
Northern Ireland	Rope	73	15	169	1,858	42 (17- 51)	8 (3- 10)	98 (39- 119)	1,081 (437- 1,313)
	Bottom	902	180	2,094	2,094	524 (212- 637)	104 (42- 127)	1,218 (493- 1,480)	1,218 (493- 1,480)
	Total	975	195	2,263	3,953	567 (229- 689)	113 (45- 137)	1,317 (533- 1,599)	2,300 (931- 2,793)
UK	Rope	2,626	525	2,967	11,947	1,528 (618- 1,856)	305 (123- 371)	1,726 (698- 2,096)	6,951 (2,814- 8,444)
	Bottom	3,314	663	8,865	8,865	1,928 (780- 2,342)	385 (156- 468)	5,158 (2,088- 6,266)	5,158 (2,088- 6,266)
	Total	5,941	1,188	11,832	20,812	3,456 (1,399- 4,199)	691 (279- 839)	6,884 (2,787- 8,363)	12,110 (4,903- 14,711

5.4.6 Total food and non-food ecosystem services

By combining the non-food ecosystem services available for valuation at present (N removal, P removal and the use of shell as aggregate, <u>Table 20</u>Table 20Y), it is possible to work out the potential value of ecosystem services under the four scenarios and compare these to the value of mussels as food. Scenario 1 demonstrates that at present the non-food ecosystem services are worth an estimated US\$20.3 million year⁻¹, compared to food costs of US\$11 million. Meanwhile, the loss of 80% of mussel production, potentially what could occur should the UK lose access to the European market, could decrease the total value of non-food ecosystem services to US\$4.1 million year⁻¹ and a food production value of US\$2.2 million. Scenario 3 and 4 examine the potential increases in ecosystem services should the mussel industry increase in size. Scenario 3, where mussel aquaculture increases to the levels of 2012 through the restoration of bottom cultured beds, led to non-food ecosystem services being worth US\$38.2 million year⁻¹ with food production generating US\$20.6 million. Scenario 4 estimated the potential non-food ecosystem services possible if mussel aquaculture across the UK were to increase through offshore rope aquaculture, once bottom culture returned to the levels of 2012. It was estimated that in this scenario, non-food ecosystem services would be worth US\$73.7 million year⁻¹, with food production generating US\$40.2 million.

		Scenario 1		Scenario 2		Scenario 3		Scenario 4	
		Food	Non-food ES	Food	Non-food ES	Food value	Non-food ES	Food value	Non-food ES
		(US\$ 000)	(US\$ 000)	(US\$ 000)	(US\$ 000)	(US\$ 000)	(US\$ 000)	(US\$ 000)	(US\$ 000)
England	Rope	146	248 (32- 450)	29	49 (5- 88)	488	831 (111- 1,503)	5,378	9,152 (1,240- 16,551)
	Bottom	1,322	2,348 (345-4,178)	264	469 (68- 835)	4,400	7,816 (1,150- 13,902)	4,400	7,816 (1,150- 13,902)
	Total	1,469	2,597 (378-4,629)	293	518 (74- 925)	4,889	8,647 (1,263- 15,406)	9,778	16,969 (2,391- 30,455)
Wales	Rope	144	244 (31- 442)	28	48 (5- 87)	368	626 (84- 1,133)	7,741	13,174 (1,785- 23,825)
	Bottom	2,740	4,867 (715- 8,658)	548	973 (142- 1,731)	7,004	12,439 (1,831- 22,128)	7,004	12,439 (1,831- 22,128)
	Total	2,884	5,112 (749- 9,102)	576	1,021 (148- 1,818)	7,373	13,068 (1,917-23,263)	14,746	25,616 (3,617-45,955)
Scotland	Rope	5,374	9,586 (1,299- 17,338)	1,074	1,916 (259- 3,467)	5,374	9,586 (1,299- 17,338)	9,814	17,510 (2,373- 31,666)
	Bottom	0	0	0	0	0	0	0	0
	Total	5,374	9,586 (1,299- 17,338)	1,074	1,916 (259- 3,467)	5,374	9,586 (1,299- 17,338)	9,814	17,510 (2,373- 31,666)
Northern	Rope	126	286 (38- 518)	25	56 (6- 103)	2,92	666 (89- 1,205)	3,220	7,337 (993- 13,269)
Ireland									
	Bottom	1,134	2,697 (396- 4,799)	226	538 (78- 959)	2,634	6,265 (921-11,145)	2,634	6,265 (921-11,145)
	Total	1,260	2,985 (435- 5,320)	252	596 (86- 1,062)	2,927	6,932 (1,013- 12,350)	5,855	13,603 (1,917- 24,415)
UK	Rope	5,791	10,370 (1,404- 18,754)	1,158	2,073 (279- 3,750)	6,524	11,714 (1,586- 21,183)	26,155	47,176 (6,395- 85,315)
	Bottom	5,198	9,914 (1,459- 17,637)	1,039	1,981 (291- 3,526)	14,039	26,522 (3,905- 47,177)	14,039	26,522 (3,905- 47,177)
	Total	10,989	20,286 (2,865- 36,392)	2,197	4,057 (571-7,277)	20,564	38,237 (5,493- 68,363)	40,194	73,701 (10,301- 132,495)

Table 20 Total value of non-food ecosystem services of mussel aquaculture in the UK converted to 2018 PPP values, under four scenarios (Scenario 1 – Status quo, Scenario 2 – Trade failure, Scenario 3 – Recovery, and Scenario 4 – Expansion).

5.5 Discussion: From Potential to Practice

This study, valuing the non-food ecosystem services of mussel aquaculture around the UK, shows the value of nutrient removal (N and P) and the use of mussel shell in aggregate, will change depending on the tonnages produced. However, there remain many ecosystem services provided by mussel aquaculture which cannot currently be included. Between 2012 to 2018, the aquaculture industry decreased in size, causing the associated ecosystem services to also decrease. Due to knowledge gaps, other non-food ecosystem services are still unable to be included within economic valuations. There is not enough information on the value of biochemical and biological accumulation within tissues and shell (van der Schatte Olivier *et al.*, 2018). There remains a wide debate on whether the storage of C in shell can be counted as sequestration due to CO_2 released during the calcification process (Filgueira et al., 2015). There remains little valuation of the value of coastal protection through bivalve beds (Borsje et al., 2011). Should these additional services be included in an economic valuation, the current estimates of ecosystem services lost would be greater.

Shell waste, historically a problem for shellfish producers, sellers, and consumers, both practically and financially has now a number of well-established markets and range of suggested uses, but is rarely utilised by the mussel aquaculture industry themselves (Ballester *et al.*, 2007; Craggs *et al.*, 2010; Morris *et al.*, 2018). Should the UK mussel aquaculture industry be able to increase production, and ensure that shell waste is utilised, large financial gains could be made.

With regard to nutrient remediation, the UK has failed to reach good ecological status for many of its rivers and the cost of reducing N from the rivers has proven to be high, both in reducing the N input into rivers, and removing it from the system. P pollution has remained an obstacle to achieving good ecological status in many surface waters around the UK (Environmental Audit Committee, 2018). Defra estimated in 2019 that in England, businesses, the third sector, and public sector jointly spent approximately US\$3.45 billion a year to protect the water environment (to prevent deterioration) and protect public health and wellbeing. This included water industry operating costs, industry and businesses investment to mitigate their potential impact on the water environment, by agriculture to meet basic regulatory requirements and reduce impacts on the water environment, and expenditure by government and the voluntary

sectors to mitigate historic damage and provide water-related benefits for people and wildlife (DEFRA, 2019).

This study proposes that whilst not the solution, mussel aquaculture is already contributing towards N and P reduction through the direct removal of these nutrients from coastal waters. Putting this into perspective, the UK mussel industry in 2018 was estimated to be worth US\$11 million year-1 (http://www.fao.org/fishery/statistics/software/fishstatj/en), and this valuation for non-food ecosystem services for the same time period shows that mussel aquaculture was providing US\$20.3 million year⁻¹. Of this US\$16.5 million could be for the removal of N from the coastal waters, and an additional US\$320,000 for the removal of phosphorus. It was also shown that the loss in mussel production from 2012 to 2018 has meant a loss of non-food ecosystem services of approximately US\$18 million. However, this could be recovered through the restoration of bottom aquaculture. Should aquaculture be expanded, as suggested by Scottish and Welsh governments, this could lead to an additional US\$35.5 million worth of non-food ecosystem services. The difficulty comes when trying to decide who pays for these services. The polluter-pays principle would suggest that the landowners who were introducing the nutrients into the transitional waters should pay for the removal (Stenis and Hogland, 2002). Alternatively, the potential role of nutrient credit trading has been considered (Ferreira and Bricker, 2018), especially on the eastern seaboard of the United States (VA Department of Environmental Quality, 2008). There has been clear evidence that filter-feeding bivalves play an important role in nutrient management, or more specifically in the management of nutrient-related issues (e.g. water clarity, eutrophication control; Carlsson et al., 2012; Haamer, 1996; Rose et al., 2015). Policy-makers have, however, been slow to embrace topdown eutrophication control mechanisms associated with commercial bivalve farming, and it is suggested that they should be part of any integrated watershed-level management strategy (Ferreira and Bricker, 2018).

The ecosystem services provided by mussel aquaculture are currently carried out freely as a by-product of the industry and have only recently been considered in terms of the water quality they provide (Hambrey and Evans, 2016). This increased water quality would greatly benefit many other coastal users, sectors, e.g. recreation and tourism, and ultimately the stability of many coastal economies (Lindahl and Kollberg, 2009; Nakamura and Kerciku, 2000; Timmermann *et al.*, 2019). It would seem that monetary indicators should not only be of interest to managers and authorities as part of a broader analysis of costs incurred for the

fulfilment of the European Union's Water Framework Directive (Andersen *et al.*, 2019), but to the mussel farmers as well.

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6 General discussion

The global review (Chapter 2, van der Schatte Olivier et al., 2018), was the first that attempted to collate all the ecosystem services carried out by the bivalve aquaculture industry and apply valuations at a global scale. Through the calculations, it was demonstrated that the non-market values were potentially worth at least 50% in addition to the global production value and highlighted that the full non-market values from the broad range of ecosystem services provided are likely to be much higher but many are not easily quantified. This found that worldwide non-food services are worth \$6.47 billion (representing 27% of the current value for bivalve meat (FAO, 2016)). This shows that even without including the other services described in this synthesis, bivalve production areas have the potential to increase the overall value of the bivalve aquaculture industry globally, while simultaneously providing environmental benefits. Since then several other studies have been published, assessing the ecosystem services of bivalve aquaculture at a range of scales. Suplicy (2018) collates several ecosystem services but does not attempt to apply valuations. A number of recent papers, however, similarly to this thesis, focus on nutrient remediation and its potential in nutrient trading (Clements and Comeau, 2019; Ferreira and Bricker, 2018; Petersen et al., 2019; Timmermann et al., 2019).

To identify important factors that could influence the nutrient remediation potential of bivalve aquaculture in the UK, **chapter 3** investigated regional variation in carbon (C), nitrogen (N) and phosphorus (P) content in tissue and shells of *M. edulis* in estuaries around the country. Of all the various environmental factors that were tested as predictors of variation in C, N, and P content of mussels, there was a significant negative relationship between P in tissue and temperature. This suggests that mussels in cooler waters have a higher percentage content P in tissue, potentially due to a temperature effect on metabolism (Smaal and Vonck, 1997; Widdows, 1973). The spatial study also found a significant negative relationship between P in shell and salinity, suggesting that the ability to remove P through shell production will be more efficient in systems with lower salinity. Despite this P in shell only contributed a small amount of total P, with the majority being removed in tissue. Therefore, in economic valuations the influence of salinity as a factor influencing P content could probably be ignored but may be useful in site specific analysis of nutrient removal potential. While not an environmental factor, the most significant influence when planning a large-scale policy approach to using mussels as nutrient remediators, was the method of culture. Rope cultured mussels removed double the

amount of N and P per tonne of harvested compared to bottom cultured mussels. Due to lower predation pressure on rope cultured bivalves (Kamermans and Capelle, 2019), there is an increased production of meat. As the tissue contained the highest proportion of nutrients, this led to significantly higher N and P content (kg tonne⁻¹) in rope cultured mussels. More C was removed in the tissue of rope-cultured mussels because of the higher meat content. However, only C incorporated in shell can be considered a long-term C store (Mangerud and Gulliksen, 1975), whilst the tissue is consumed and respired. Our study found that despite having a similar weight of carbon removed at both bottom and rope cultured mussels, there was significantly more carbon removed in the shell of bottom cultured mussels. This would indicate that future developments focusing on nutrient remediation would look to utilise suspended rope mussel aquaculture due to the potential higher nutrient yield per area, with growth being focussed in the tissues. Furthermore, intertidal sites have limited potential due to area constraints and competition with other users, whilst offshore, using rope methods, has greater potential and less conflict with other users and already there are large offshore sites already being developed off the south coast of England (Sheehan et al., 2020). Whilst bottom culture mussel farmers continue to collect mussel spat to re-seed beds, it is unlikely there will be any expansion of these due to the current preference to go offshore. Offshore mussel aquaculture comes with large investment costs, although due to increased production per area, and rate of growth of the mussels, this can often be justified. I would expect that in the next decade there will be a large number of offshore sites being developed and operating around the UK.

With the information collected, **chapter 5** collates all the information together from across the thesis to look at four potential future scenarios for the mussel aquaculture industry. Utilising tonnages of mussels produced in the UK combined with the average values of C, N and P that were calculated around the UK in **chapter 3**. This included values for both bottom and rope cultured mussels as these were found to be significantly different. between bottom and rope culture. These were combined with economic values for N and P removal, and the use of shell as aggregate that was found during the global review (**chapter 2**, van der Schatte Olivier *et al.*, 2018). It was found that not only has the aquaculture industry decreased in size but as a result, the ecosystem services it provides have decreased as a result. When looking at a scenario of market loss there could be a major reduction in the tonnage of mussels produced and associated services with only 24,000 kg of N and 200 kg of P removed year⁻¹. Alternatively, other potential scenarios that were assessed included restoring bottom cultured mussels to the levels they had

been previously which showed that this would increase N and P removal by 83% and 53% respectively. When assessing the potential N and P removal that could be achieved by doubling aquaculture from a restored bottom culture level, it was found that this could lead to N and P removal increases of 265% and 300% from what is currently being removed.

In addition to nutrient remediation it was calculated that at present the UK is producing around 6,000 tons of shell in the mussel industry, which if marketed could be a valuable commodity. This would most likely be by marketing shell for use as an aggregate replacement, although there are studies looking into other options such as agricultural liming. Should bottom culture be returned to the levels of 2012 (Scenario 3), or expanded further through offshore sites, then potentially it would be possible to produce anywhere from 12,000 - 21,000 tonnes of shell, increasing the potential of this market greatly.

The period during which mussel farmers harvest is based on a combination of market demands but also meat quality, avoiding harvesting following spawning events as there is a reduced meat condition (Pérez Camacho *et al.*, 1991). It was found that temporal change had a significant effect on the amount of N and P removed in harvested mussels (**Chapter 4**). Most of the removed N and P was held within the tissues, with a small amount in shell. Our results show that if mussels were to be used for nutrient remediation, the most effective time to harvest them to remove the most N and P from the system would be directly before spawning or once the mussels had recovered following spawning. The implication of this on nutrient remediation schemes using bivalves is that the seasonal variation is an important factor to consider when deciding when to harvest. If harvested in the spring before spawning takes place, it is possible to remove 25% more N and 50% more P. The sites used in **chapter 4** were situated close together, but at a UK wide level, the time of this spawning is likely to vary temporally, as different areas are subject to different environmental regimes. This would in turn mean that the policy of when to harvest mussels to remove nutrients would have to vary spatially around the country to coincide with spawning.

At present the future of mussel aquaculture is entering a new phase in the UK and around the world. The industry is looking to the offshore environment to expand its potential production; offshore has less competition for the space and for the public it is an out of sight, out of mind system. With this come the costs of setting up sub surface long lines at the cost of millions of pounds. The benefits have been seen to make this worthwhile, however, with offshore rope grown mussels quickly reaching market size and being less gritty as they are

grown in the water column. Additionally, as the mussels are away from the coastline, there is less need to be concerned about human derived pathogens infecting the shellfish. Currently, the UK exports around 80% of its mussels to Europe and whilst there is the potential to export more at present, as the trade relationships with Europe adjust to the UK's new position outside of the European Union, it is very difficult to anticipate what will happen.

The potential expansion to offshore would provide a number of ecosystem services, but the concept of how to market ecosystem services remains complex. Bivalve aquaculture has been shown through a wide range of literature to have many positive ecosystem services. Yet, whilst this is acknowledged by policy makers, there has been no real practical breakthrough in actually paying for the services, or accounting for the services in decision making. Additionally, it is important to assess negative ecosystem services in conjunction to the positives. The main negative service is that, in some cases below the rope mussels there can build up a mussel mud, made up of the faeces and pseudofaeces. This could alter the ecosystem that is currently on the seabed, affecting the ecosystem services that the system provides, although, with proper assessment of site suitability, the impact of this can be kept to a minimum (Mizuta et al., 2019).

The ecosystem services highlighted within this thesis, if paid for, would triple the current value of the UK mussel aquaculture. If knowledge gaps could be addressed and the potential value of other ecosystem services included, the potential value of the UK mussel aquaculture industry would be far greater still.

6.1 Knowledge gaps

The biological functions performed by bivalves are generally well-understood, however, there remain knowledge gaps that still need to be addressed. For example, the supporting ecological functions and trophic interactions supported by bivalves have only been studied extensively in the USA for one species: oysters. Therefore, for the supporting services, more basic quantification of processes is required to allow upscaling for other species and in other contexts.

The spatial survey carried out around the UK found that rope cultured mussels removed double the amount of N and P per tonne of harvested compared to bottom cultured mussels. The calculations, however, did not account for growth rates, which previous studies have shown are faster in rope cultured mussels than bottom cultured. While average seawater temperature did not influence nutrient content of mussels positively, it should, be noted that warmer temperatures will support faster growth and therefore a higher rate of nutrient removal. Similarly, while there is more carbon trapped in the shell of bottom cultured mussels, this may be offset by the greater growth rate expected in rope-cultured mussels.

The temporal study within this thesis found that mussels which are situated more subtidally have greater potential as nutrient remediators than intertidal mussels higher up the shore. This would indicate that further work could be carried out to assess the comparative cost-effectiveness of nutrient removal from constantly submerged rope cultured mussels compared to intertidal or subtidal benthic farms.

In terms of provisioning services, currently the most accurate data available for upscaling at a country or global level relies heavily on official statistics. This inherently may under-record landed bivalves due to the contribution of small-scale and subsistence aquaculture (FAO, 2016). There is still no comprehensive data on use of shell in poultry grit, in aggregate, or of bivalve waste as a fertiliser. Whilst these are all potential options, their use in valuations remains complicated and hypothetical. Much of the information on bivalve regulating services is based on oysters in the USA and mussels in the Baltic, and their ability to remove N and P. This thesis now provides a UK wide overview of the nutrient remediation carried out, but only at a simple level of direct removal through harvest. More work is still required to assess the potential importance of in situ services, such as denitrification and burial of nutrients in the sediment, not just those based purely on harvest and removal. There remains little data from other regions in the world and for other species and it is still uncertain whether N and P removal rates differ regionally/globally. The findings of this thesis have shown that Asia has the greatest potential in terms of nutrient remediation, but still there are relatively few studies available on this. Similarly, the USA remains the only country with published estimates of the role of bivalves in coastal protection. Finally, cultural services are still among the most difficult to classify and value. Studies are beginning to investigate their importance, but this is only in a handful of papers.

6.2 Conclusion

Bivalve aquaculture provides a wide variety of ecosystem services, beyond their traditional market value. Attempts to value these services are still at an early stage, with this thesis unable to apply values for ecosystem services other than the nutrient removal of N and P, and the use

of shell as aggregate (Carrs *et al.*, 2020; van der Schatte Olivier *et al.*, 2018). It was possible to investigate regional variation around the UK and attempt to unravel the environmental characteristics that led to differences in the mussels. It was discovered that the method of culture makes a significant difference to the potential remediation carried out. Finally, through a temporal study at two sites, it was found that the mussel carbon, N, and P content followed similar patterns and that the best time to harvest, in terms of remediation was before they spawned. The results of this thesis raised the possibility of further areas of research, looking into the variation between rope and bottom cultured sites on a temporal scale, in order to improve the understanding of mussel aquaculture as a tool for nutrient remediation.

7 Appendix A

Species	Size of organisms (mm)	Pumping rates per individual bivalve (l h ⁻¹)	Source
Mytilus edulis	30-40	0.75–1.20	Jones <i>et al.</i> (<u>1992</u>)
Mytilus edulis	25.5	0.80	Quraishi (<u>1964</u>)
Mytilus edulis	48	1.06	Willemsen & Willemson (1954)
Crassostrea virginica	100	34.00	Loosanoff & Nomejko (<u>1946</u>)
Crassostrea virginica	100	26.00	Nelson (<u>1935</u>)
Mya arenaria	70	0.95	Allen (<u>1962</u>)
Venus mercenaria	40	2.07	Coughlan & Ansell (<u>1964</u>)
Venus striatula	20	0.12	Allen (<u>1962</u>)
Cardium edule	30–40	0.50	Willemsen & Willemson (1954)

 Table A 1 Shellfish pumping rates from literature of laboratory-based experiments

Species	Location	Density (individuals m ⁻²)	Summary of findings	Source
Crassostrea virginica	South Carolina estuaries, USA	217–2,831	Removed 28% of chlorophyll α in situ (40.7% in laboratory experiment)	Grizzle <i>et al</i> . (<u>2008</u>)
Crassostrea gigas	Thau Lagoon, France	40	Removed 56 to 86% of chlorophyll α	Souchu <i>et al.</i> (<u>2001</u>)
Crassostrea gigas	Moreton Bay, Australia	33–100	Removed 92% of chlorophyll α	Jones & Preston (<u>1999</u>)
Mytilus edulis	Menai strait, Wales	-	Removed 69% of chlorophyll α	Morioka <i>et al.</i> (<u>2017</u>)
Corbicula japonica	Lake Shinji, Japan	0–1,000	Removed 60% of chlorophyll α	Nakamura & Kerciku (<u>2000</u>)
Corbicula fluminea	Potomac River, USA	1.2–1,467	Removed 30% of chlorophyll α	Cohen <i>et al</i> . (<u>1984</u>)

Table A 2 Chlorophyll $\boldsymbol{\alpha}$ removal by bivalves

	Total	NH ₄ -N	Phosphate	Potash	Sulphur (as	Magnesium (as
	Nitrogen		P ₂ O ₅	(K ₂ O)	SO 3 ⁻)	MgO)
	(N)					
Whelk	22.6	0.51	2.6	2.7	10.3	1.0
waste						
Nephrop	14.9	0.89	7.0	2.0	2.8	2.1
waste						
Crab waste	18.7	0.49	7.2	1.1	3.0	6.8
Scallops	16.8	1.18	1.8	1.6	4.4	1.1
waste						
Cattle	6.0	1.1	3.5	8.0	1.8	0.7
manure						
Sewage	7.5	1.0	930	Trace	6.0	1.3
sludge cake						
Green waste	7.0	0.2	2.8	5.3	3.5	3.8
compost						
Shellfish-	10.0	0.5	4.1	4.2	ND	ND
based						
compost						

Table A 3 Major crop nutrients in fisheries and aquaculture wastes compared with traditional organic manures (kg per tonne of fresh weight; ND represents no data) taken from ADAS UK Ltd (2006)

Seafood Festival	Location	Number of
		visitors
USA		
Asbury park Oysterfest	Asbury Park, New Jersey	~10,000
Austin oyster festival	Austin, Texas	~2,000
Ballard Seafood Fest	Seattle, Washington, USA	~75,000
Bodega seafood festival	Bodega, California	~10,000
Boston Seafood Festival	Boston, Massachusetts	~7,500
Chesapeake Bay crab and beer Festival – Baltimore	Baltimore, Maryland	~4,000
Chesapeake Bay crab and beer Festival – Washington DC	Washington DC	~7,000
Chesapeake Bay maritime museum Oyster festival	St. Michaels, Maryland	~4,500
Chesapeake Bay maritime museum Watermen's Appreciation Day	St. Michaels, Maryland	~3,500
Good Catch Oysterfest	Charleston, South Carolina	~400
Louisiana seafood Festival	New Orleans, Louisiana	~55,000
Lowcountry Oyster Festival	Mount Pleasant, South Carolina	~10,000
Milford Oyster Festival	Milford, Connecticut	~50,000
Mount Dora Seafood Festival	Mount Dora, Florida	~50,000
North Carolina seafood festival	Morehead City, North Carolina	~200,000
Ocean State Oyster Festival	Rhode Island	~1,500
Poquoson seafood festival	Poquoson, Virginia	~50,000

Table A 4 Examples of seafood festivals in five countries, and the number of visitors reported at each festival

Table A 4 continued.

Port Fish Day Festival	Port Washington, WI	~50,000
Potomac Jazz and Seafood Festival	Coltons Point, Maryland	~1,000
Riverwalk Stone Crab & Seafood Festival	Fort Lauderdale, Florida	~7,000
Rockport-Fulton Sea Fair	Rockport, Texas	~15,000
Roscoe village Oyster Festival	Chicago, Illinois	~8,000
Salmonfest Alaska Festival	Ninilchik, Alaska	~8,000
India Point Seafood Festival	India Point, Rhode Island	~5,000
Sensible Seafood Fest	Virginia Beach, Virginia	~600
Washington Oyster festival	Shelton, Washington	~15,000
Wellfleet Oyster festival	Wellfleet, Massachusetts	~25,000
Yarmouth Clam Festival	Yarmouth, Maine	~100,000
	Subtotal	~775,000
Australia		
Ballina Prawn Festival	Ballina, New South Wales	~10,000
Mandurah Crab Fest	Mandurah, Western Australia	~120,000
Narooma Oyster Festival	New South Wales, Australia	~4,000
Taste of Tasmania	Hobart, Tasmania	~115,000
Tin Can Bay Seafood Festival	Tin Can Bay, Queensland	~10,000
	Subtotal	~259,000
Republic of Ireland		
Seafest Festival	Galway, Ireland	~101,000
	Subtotal	~101,000

Table A 4 continued.

Jamaica		
Little Ochi Seafood Festival	Jamaica	~650
	Subtotal	~650
United Kingdom		
Clovelly Lobster and Crab Feast	Clovelly, Devon	~1,500
Crabstock	Chippenham	~4,000
Cromer and Sheringham Crab and Lobster Festivals	Cromer, Norfolk	~20,000
Fishstock	Brixham, Devon	~5,000
Isle of Man Queenie Festival	Isle of Man	~4000
Menai Seafood Festival	Menai Bridge, Wales	~12,000
Newlyn Fish Festival	Newlyn, Cornwall	~15,000
Newquay Fish Fest	Newquay, Cornwall	~10,000
Paignton Harbour day	Paignton, Devon	~5,000
Pembrokeshire Fish Week	Pembrokeshire, Wales	~30,000
Plymouth Seafood Festival	Plymouth, Devon	~12,000
Pommery Dorset Seafood Festival	Weymouth, Dorset	~50,000
Rock Oyster Festival	Rock, Cornwall	~3,000
Whitstable Oyster Festival	Whitstable, Kent	~80,000
	Subtotal	~251,500
Total		~1,387,150

8 Appendix B

Table B 1 Supplementary Material 1 Best linear model for percentage content of C, N and P and kg of C, N and P in shell and tissue. Asterisks indicate parameter significance. * GLM, p≤0.05, ** p≤0.01, *** p≤0.001.

Model	Response	Best Linear Model	Adjusted R ²	Model
Number	Variable		value	Significance
1	%C in tissue	culture type*	0.3087	$P \le 0.001$
3	%P in tissue	culture type* and mean annual	0.4855	$P \le 0.05$
		seawater temperature*		
4	%C in shell	culture type* and salinity	0.4841	$P \le 0.001$
5	%N in shell	culture type*	0.3031	$P \le 0.001$
6	%P in shell	Salinity*	0.2367	$P \le 0.01$
7	Kg C in tissue	culture type*	0.5272	$P \le 0.001$
8	Kg N in tissue	culture type**	0.5464	$P \le 0.001$
9	Kg P in tissue	culture type***	0.6309	$P \le 0.001$
10	Kg C in shell	culture type**	0.5587	$P \le 0.001$
12	Kg P in shell	culture type**	0.4728	$P \le 0.001$

Table B 2 Mean ± SE of the upscaled carbon, nitrogen and phosphorus content, kg tonne-1 live mussels harvested. * indicates rope cultured mussels.

ID	Site name	C in tissue	N in tissue	P in tissue	C in shell	N in shell	P in shell	Whole mussel	Whole mussel	Whole mussel
								С	Ν	Р
1	Cromarty Firth	16.37±0.80	3.67±0.18	0.45±0.02	61.16±0.67	1.85±0.02	0.03±0.000	77.53±0.44	5.52±0.16	0.50±0.02
2	Lindisfarne	11.06±0.40	2.35±0.09	0.35±0.01	61.07±0.76	1.38±0.02	0.03±0.000	72.14±0.94	3.73±0.09	0.41±0.01
3	River Coquet	13.89±0.71	2.87±0.15	0.39±0.02	59.11±1.02	2.43±0.04	0.03±0.000	73.00±1.46	5.30±0.17	0.44±0.02
4	Deben Estuary	12.84±0.64	2.64±0.132	0.30±0.02	60.65±0.46	2.18±0.02	0.03±0.000	73.49±0.83	4.82±0.13	0.37±0.02
5	Lyme Bay *	49.11±2.23	9.75±0.44	1.10±0.05	45.19±2.09	1.94±0.09	0.02±0.001	94.30±4.25	11.68±0.53	1.14±0.05
6	River Teign	15.78±0.61	3.19±0.12	0.35±0.01	57.04±2.47	2.07±0.09	0.03±0.001	72.82±1.95	5.26±0.06	0.40±0.01
7	River Fowey *	29.97±3.41	7.13±0.88	1.12±0.13	57.25±1.16	2.01±0.04	0.02±0.000	87.22±3.85	9.14±0.13	1.16±0.13
8	River Fal	19.99±3.15	4.19±0.66	0.51±0.08	73.24±15.25	3.03±0.63	0.04±0.009	74.72±1.97	5.93±0.29	0.50±0.03
9	Swansea Docks *	16.08±0.90	3.35±0.19	0.46±0.03	40.98±2.02	1.74±0.09	0.02±0.001	57.06±2.87	5.09±0.27	0.50±0.03
10	Milford Haven	9.21±0.38	1.98±0.08	0.20±0.01	61.07±2.16	1.53±0.05	0.03±0.001	70.27±1.87	3.51±0.05	0.27±0.01
11	Afon Braint	13.80±1.63	2.74±0.32	0.36±0.04	67.56±1.29	1.68±0.03	0.04±0.001	81.36±1.13	4.42±0.30	0.44±0.04
12	Menai Strait	21.84±1.62	4.22±0.31	0.52±0.04	50.05±1.46	1.97±0.06	0.03±0.001	71.89±2.76	6.18±0.35	0.58±0.04
13	River Ribble	14.22±0.73	3.05±0.16	0.29±0.02	65.98±1.58	2.24±0.05	0.03±0.001	80.20±1.12	5.29±0.12	0.35±0.01
14	Loch Leven *	30.46±1.61	5.71±0.30	0.94±0.05	41.04±0.77	2.36±0.04	0.03±0.001	71.50±2.06	8.07±0.32	1.00±0.05
	Average for rope	31.40±2.88	6.48±0.58	0.90±0.07	46.12±1.69	2.01±0.06	0.04±0.001	77.52±3.65	8.50±0.59	0.95±0.07
	cultured mussels									
	Average for bottom	14.59±0.55	3.02±0.11	0.69±0.01	60.15±0.77		0.06±0.001	74.74±0.68	5.00±0.13	0.43±0.01
	cultured mussels					1.97 ± 0.05				
	Mean ± SE	19.39±1.28	4.01±0.26	0.52±0.04	56.14±1.05	1.98±0.04	0.03±0.001	75.54±1.14	6.00±0.27	0.58±0.04



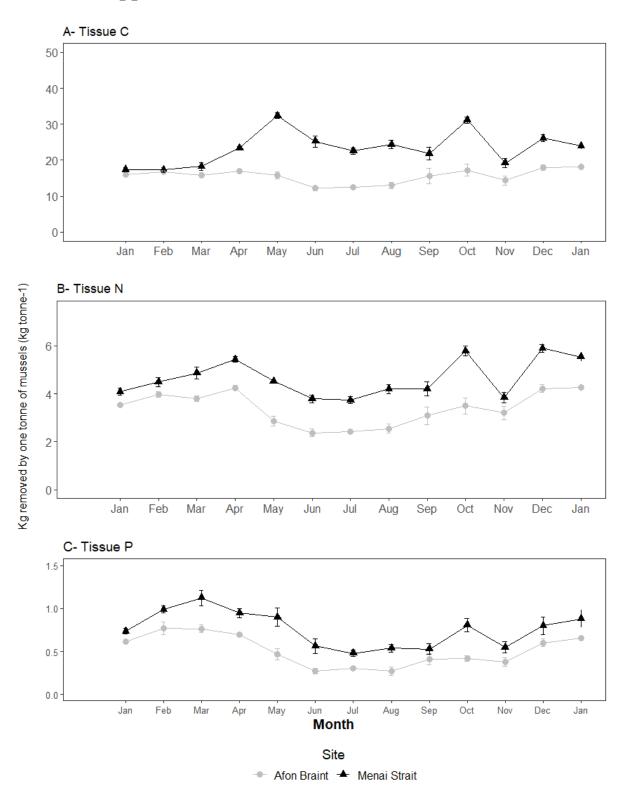


Figure C 1 Kg of carbon (A), nitrogen (B) and phosphorus (C) in tissue per tonne of live mussels removed (with SE bars) for the Afon Braint and Menai Strait, plotted against month

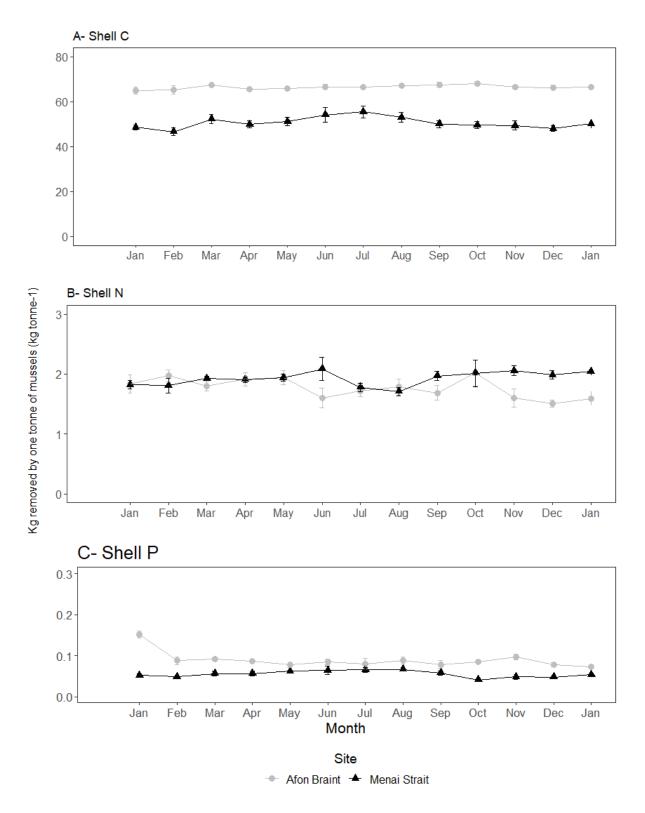


Figure C 2 Kg of carbon (A), nitrogen (B) and phosphorus (C) in shell per tonne of live mussels removed (with SE bars) for the Afon Braint and Menai Strait, plotted against month.

10 Appendix D: Ecosystem services provided by a non-cultured

shellfish species: the common cockle Cerastoderma edule

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10.1 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 wildharvested 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'.

10.2 Keywords:

Bivalve; Ecosystem engineer; European coastal biodiversity management; Nutrient removal; Carbon sequestration; Cultural services

10.3 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, 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 noncultured 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 m² 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.

10.4 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 wideranging 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 et al., 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 \$3,583 (range: \$2,827-4,303) 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: \$8,996-31,050 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 1,138 (range: $538-1738 t^{-1}$).

10.5 Results and discussion

10.5.1 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.

10.5.1.1 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 ($\leq 8^{\circ}$ 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 = 11.60W^{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⁻¹h⁻¹. Mean clearance rates standardised by shell length were 6.03 (± 0.81) Lind⁻¹h⁻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 - 55% of the maximum values observed in laboratory experiments.

10.5.1.2 Perturbation and alteration of sediment properties

From a functional point of view, cockles are classified as surficial biodiffusers, inducing diffusive-like sediment reworking and bioirrigation 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, 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, 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.*, 2012). 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, 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).

10.5.1.3 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, 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.

10.5.2 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.

10.5.2.1 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 D1).

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 2014-17 varied between 14,000 - 26,000 tonnes (Table D1), 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 \$1,355 t⁻¹ (range: \$1,145-1,588 t⁻¹) for scallops (Marine Management Organisation, 2017).

Table D 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	5,036	5,997
Denmark	6,081	7,699	5,917	7,924
Portugal	1,991	4,700	1,835	5,063
Spain	1,195	2,410	1,561	2,846
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

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).

10.5.2.2 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.

10.5.2.3 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).

10.5.2.4 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 \$2,400 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 (Figure 1a).

10.5.3 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)' \approx carbon sequestration, 'Water conditions $(2.2.5.2) \approx$ Salt water quality through filtration, 'Regulation of baseline flows and extreme events' $(2.2.1.1) \approx$ erosion control, 'Pest and disease control' $(2.2.3.2) \approx$ 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' $(2.1.1) \approx$ pathogen and toxin removal.

10.5.3.1 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.

10.5.3.2 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.

10.5.3.3 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).

10.5.3.4 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).

10.5.3.5 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.

10.5.4 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.

10.5.4.1 Physical and experiential

Perhaps the most common manifestation of this was the ubiquitous value attached to familyfocused 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.

10.5.4.2 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 (Figure 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 (Figure 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 (Figure 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.

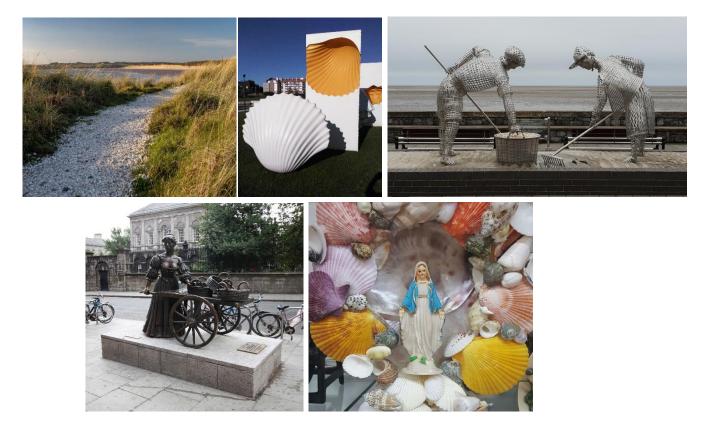


Figure D 1 Ecosystem service examples: cockles. Clockwise from top left: (a) cockle shells used on footpath on Ynys Llanddwyn, Wales © Andrew van der Schatte Olivier; (b) 'Ovos Moles' sculpture in Aveiro, Portugal © Laurence Jones; (c) 'The Cocklepickers' by Michéal McKeown in Blackrock, Co. Louth, Ireland. 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,)].

10.5.4.3 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 Figure 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).

10.5.4.4 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.

10.5.5 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 D2 and the potential economic value in Table D3. The largest non-food value is ascribed to shell waste. Annually 5,543 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.

Country	Total tonnage landed	Meat	Weight shell	of Nitrogen remediated	Phosphorus remediated
Denmark	5,917	1,065	1,827	17.3	1.7
France	1,896	341	585	5.5	0.6
Ireland	222	40	69	0.6	0.1
Italy	56	10	17	0.2	0.0
Portugal	1,958	352	605	5.7	0.6
Spain	2,623	472	810	7.7	0.8
United Kingdom	5,037	907	1,555	14.7	1.5
Total	18,027	3,188	5,469	51.7	5.1

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

Country	Meat	Shell as aggregate	Nitrogen remediation	Phosphorus remediation	Total value of ecosystem services
Denmark	\$38.1 (30.1-45.8)	\$21.1	\$3.5	\$0.6	\$63.3
		(10.0-32.2)	(1.6-5.4)	(0.2-1.0)	(41.9-84.4
France	\$12.2 (9.6-14.7)	\$6.8	\$1.1	\$0.2	\$20.3
		(3.2-10.3)	(0.5-1.7)	(0.1-0.3)	(13.4-27.0)
Ireland \$1.	\$1.5 (1.1-1.8)	\$0.8	\$0.1	\$0.0	\$2.4
		(0.4-1.2)	(0.1-0.2)	(0.0-0.0)	(1.6-3.2)
Italy	\$0.4 (0.3-0.4)	\$0.2	\$0.0	\$0.0	\$0.6
		(0.1-0.3)	(0.0-0.1)	(0.0-0.)	(0.4-0.8)
Portugal \$12.7 (\$12.7 (10.0-15.2)	\$7.0	\$1.1	\$0.2	\$21.0
		(3.3-10.7)	(0.5-1.8)	(0.1-0.3)	(13.9-28.0)
Spain	\$17.0 (13.3-20.3)	\$9.3	\$1.5	\$0.3	\$28.1
		(4.4-14.3)	(0.7-2.4)	(0.1-0.4)	(18.5-37.4)
United	\$32.5 (25.6-39.0)	\$17.9	\$2.9	\$0.5	\$53.8
Kingdom		(8.5-27.4)	(1.3-4.6)	(0.2-0.9)	(35.6-71.9)
Total	\$114.3 (90.2-137.2)	\$63.1	\$10.3	\$1.8	\$189.5
		(29.8-96.3)	(4.6-16.0)	(0.7-3.0)	(125.3-252.6)

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

10.6 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, 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 (Verje *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 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.

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