Bioremediation of waste under ocean acidification: reviewing the role of *Mytilus edulis*

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Abbreviations

AE: Absorption efficiency

BW: Bioremediation of waste

CR: Clearance rate

OA: Ocean acidification

Abstract

Waste bioremediation is a key regulating ecosystem service, removing wastes from ecosystems through storage, burial and recycling. The bivalve *Mytilus edulis* is an important contributor to this service, and is used in managing eutrophic waters. Studies show that they are affected by changes in pH due to ocean acidification, reducing their growth. This is forecasted to lead to reductions in *M. edulis* biomass of up to 50 % by 2100. Growth reduction will negatively affect the filtering capacity of each individual, potentially leading to a decrease in bioremediation of waste. This paper critically reviews the current state of knowledge of bioremediation of waste carried out by *M. edulis*, and the current knowledge of the resultant effect of ocean acidification on this key service. We show that the effects of ocean acidification on waste bioremediation could be a major issue and pave the way for empirical studies of the topic.

Keywords: Bioremediation, Mytilus edulis, ocean acidification, waste, experiments, ecosystem service

1. Introduction

Ecosystem services are *ecological components directly or indirectly consumed or enjoyed to produce human well-being* (Boyd and Banzhaf, 2007) and this concept has become key to linking economic and ecological sciences in support of sustainable environmental management (Fisher et al., 2008). Bioremediation of waste (BW) is an important regulating ecosystem service and can be defined as removal of waste from the environment through storage, burial and recycling (Beaumont et al., 2007). It results in cleaner and less turbid water, a final ecosystem service with positive effects on other services too (MEA, 2005). For example, BW supports the services of food provision by creating conditions for healthy fisheries and aquaculture products, and recreation and amenity through its contribution to bathing water quality. Also, deeper light penetration due to clearer water allows marine benthic flora to sequester carbon up to a greater depth than in turbid waters (Burkholder and Shumway, 2011; Irving and Connell, 2002).

In the marine environment many animal taxa and guilds are involved in BW. For example, marine microbes occur in all habitats, degrading organic detritus and recycling nutrients (Munn, 2004). Bioturbators and bioirrigators, such as burrowing shrimps or polychaetes, can draw wastes deep into the sediment leading to removal of wastes by burial (Volkenborn et al., 2007; Queirós et al., 2013). In addition, most living organisms can sequester wastes into their tissues (Norkko and Shumway, 2011; Queirós et al., 2013). Filter feeding is an important trophic mode in many marine invertebrates and a key process in BW. Filter feeders actively pump large volumes of water over a filter that collects highly dilute material for feeding (Riisgard and Larsen, 1995). In this way they improve water quality by removing suspended particles (seston) from the water column (Grizzle et al., 2008). Filter-feeding molluscs are often found in dense populations and can profoundly influence pelagic and benthic processes as well as add to benthic-pelagic coupling, the movement of nutrients between the sediment and overlying water (Ward and Shumway, 2004; Layman et al., 2014). They transform the filtered material into somatic and reproductive growth, and aid the deposition of particulate matter to the benthos through faeces and pseudofaeces (Ward and Shumway, 2004).

Many filter feeding bivalves are vulnerable to changes in the marine environment particularly a reduction of ocean water pH, known as ocean acidification (Kroeker et al., 2013; Parker et al., 2013). Ocean acidification is caused by rising atmospheric carbon dioxide (CO_2) levels due to anthropogenic activities such as the burning of fossil fuel, cement production and deforestation. Carbon dioxide dissolves into ocean surface waters, reducing atmospheric CO_2 concentrations but at the same time decreasing the pH of ocean surface waters. Since the beginning of global industrialisation the pH of the oceans has decreased by 0.1, equivalent to a 26% increase in acidity (Aze et al., 2014). All Earth System Models calculated for the IPCC 5th Synthesis report project a continued global decrease in ocean pH by the end of the 21st century and beyond (IPCC, 2014). A reduction of pH also leads to changes in ocean carbonate chemistry, reducing the carbonate ions (CO_3^{2-}) and lowering the calcium carbonate ($CaCO_3$) saturation of seawater. This leads to reduced availability of $CaCO_3$ for marine calcifiers (Parker et al., 2013). These changes to ocean carbonate chemistry and pH have large effects on marine animals which have been the focus of sustained research effort in recent years (Melzner et al., 2011; Hüning et al., 2013; Kroeker et al., 2013; Parker et al., 2013; Thomsen et al., 2013; Aze et al., 2014). A meta-analysis of the effects of a pH reduction by 0.5 showed negative effects on survival, calcification, growth, development and abundance for ten taxonomic groups including calcifying and non-calcifying algae and animals (Kroeker et al., 2013). For fauna, the meta-analysis compared phyla only. Findings for molluscs (drawn mostly from studies on bivalves) indicate that they are particularly badly affected. Effects include significant reductions in adult and larval survival, growth and mean reduction of calcification.

Calcifying species play key roles in ecosystem functions (Barry et al. 2011). They may provide services to other species, for example, through the provision of habitat or by their contribution to waste remediation. The role of species vulnerable to OA in these services is not yet fully explained and therefore predicting the effect of OA on these services difficult (Cooley et al. 2009). If such species are affected by OA, cascading changes may result in the services that they provide and this even before extinction occurs (Barry et al. 2011).

This research focuses on the bivalve mollusc *Mytilus edulis*. *They* are common in the Atlantic from the Arctic to the Mediterranean, with a habitat range from the upper shore to the shallow subtidal (Hayward and Ryland, 1995). They can also be abundant, for example dominating sessile assemblages on off-shore structures (Krone et al. 2013). *M. edulis* form an interesting case study because they are such effective filter feeders that they are used to manage eutrophic waters, (Lindahl et al. 2005). This shows that they can play a substantial role in the bioremediation of waste (Lindahl et al. 2005). As calcifiers, using the carbonate ions from seawater to form protective shells, they are also known to be vulnerable to changes in OA (Kroeker et al., 2013). Their capacity to continue calcification and maintaining their shells intact under predicted low pH scenarios has been widely studied and reductions in several key physiological functions of *M. edulis* under OA scenarios have been shown (Kroeker et al., 2013).

In 2013 the global production of *M. edulis* was 197 831 tons with a value of US$ 434,305 (FAO, 2015). While the economic impacts of ocean acidification are not well studied, reduced growth in *Mytilus edulis* as a consequence of OA can be assumed to have socio-economic impacts. For example, in a review of the potential impacts of OA on Mediterranean countries, Hilmi et al. (2014) noted a strong impact of ocean acidification on *Mytilus* species (*edulis* and *galloprovincialis*) and suggested that this may particularly affect artisanal fishermen and aquaculture farmers. For impacts on mollusc aquaculture, Narita et al. (2012), estimate global annual losses of US$6 billion under constant demand and US$100 billion if demand increases in line with future income increase. Similarly, Cooley and Doney (2009) estimate an annual loss to the US of US$75-187 million of direct revenue from decreasing mollusc harvests between 2007 and 2060 (according to the future CO_2 regime used and the discount rate applied). This would be in addition to the impacts felt from temperature changes. For example, in the summer of 2003 a heatwave in French waters led to massive *M. edulis* spat die-off (FAO, 2015). Such events, coupled with low ocean pH may lead to reduced *M. edulis* production. This in turn will reduce their capacity to act for bioremediation with further impacts on ecological functioning and wider ecosystem service delivery.

While both the filtration capacity of filter feeding bivalves, and the effect of OA on calcifying organisms such as *M. edulis* have been extensively studied (e. g. Melzner et al., 2011; Thomsen et al., 2013; Aze et al., 2014), little work focuses on the effect of OA on the filtration capacity of bivalves. To our knowledge, there are no studies on the effect that OA may have on the ecosystem service of BW. Hence, this review was timely.

This study aims to answer the following research questions:

1. How do filter feeding bivalves *M. edulis* contribute to BW?
2. What are the key effects of OA on *M. edulis*?
3. How does OA affect BW of *M. edulis*?

The paper is structured around these three research questions. Section 2 defines how *M. edulis* filter feed, followed by examples of wastes and how they are bioremediated by *M. edulis*. Section 3 summarises research into effects of OA on *M. edulis* which are likely to reduce their ability to bioremediate waste. The effects of OA on their primary food source, phytoplankton, are also briefly discussed. Section 4 addresses the third research question using examples of modelling studies carried out on *M. edulis*. In the Discussion (Section 5), changes to management options as well as human health implications of eating *M. edulis* under OA are summarised.

2. How do filter feeding bivalves *M. edulis* contribute to BW?

Mussels of the genus *Mytilus* occur worldwide on many coasts. They dominate hard substratum communities and have a well-developed and efficient filtering system (Brzozowska et al., 2012). They often dominate fouling communities in the shallow subtidal as well, and provide important secondary habitat on hard substrata. For example, measurements of *M. edulis* biomass on offshore wind energy structures showed that they can cover the structures with up to 3.4 kg of biomass m^{-2} (Krone et al. 2013). They can lead to ecosystem changes because of their filtration capacity (Krone et al. 2013), removing large quantities of phytoplankton and therefore nutrients, reducing effects of eutrophication as well as sediment, harmful bacteria and contaminants (Birkbeck and McHenery, 1982; Krone et al., 2013). Bivalves, particularly mussels, are often used for contaminant monitoring due to their filtration rates, sessile lifestyle and because they can dominate hard substrata both in terms of weight and abundance compared to other sessile species (Widdows et al., 1995). For example, they have been used to study the fate of persistent organic pollutants (McEneff et al., 2014) and metal pollution (Chase et al., 2001).

2.1 Defining and assessing filter feeding in *M. edulis*

To understand the role that *M. edulis* plays in the delivery of bioremediation of waste it is first necessary to understand how filtration is documented in the literature. The literature provides a range of measures for bivalve filtration but they are not clearly defined or consistently used. While this diversity of filtration parameters in *M. edulis* is beneficial to understanding their capacity for BW, it also makes it difficult to compare measurements from different studies. Table 1 lists definitions used by different authors as well as units of measurements and it highlights the inconsistencies as concerns definitions and units.

The most basic parameter to describe filtration physiology in *M. edulis*, particularly for application in coastal management measures, is filtration or pumping capacity (from now on filtration capacity). This measures the amount of water going through a filter feeder or through an assemblage of filter feeders in a set amount of time (Lindahl et al., 2005). One way to measure filtration capacity is to measure the size of the exhalant siphon as this is controlled by the size of the animal and *M. edulis* can also adjust it by closing their valves when necessary (Møhlenberg and Riisgård, 1978; MacDonald et al., 2011; Riisgård et al., 2011). They reduce the size of the gape when phytoplankton cell concentrations are too high or too low for their optimal feeding ratio (Riisgård et al., 2011). This measure does not incorporate recirculation of water that has already been taken up by other individuals or themselves. However, it is important to know the volume of water that has been recirculated as it reduces the efficiency of *M. edulis* to filter large volumes of unfiltered water.

Clearance rate, filtration rate, and assimilation efficiency (sometimes called absorption efficiency, from now on assimilation efficiency) are also used to describe filter feeding efficiency and are measured depending on the question addressed in a particular study. Clearance rate (CR) is a common indicator of *M. edulis* feeding activity and measures the amount of seston removed from the water. In experiments, this is done by subtracting seston mass remaining in the outflow of a treatment chamber containing an individual of a *M. edulis*, from the seston mass measured in the outflow of a control chamber that contains no animal (MacDonald et al., 2011). Rather than measuring the mass of seston lost per time (for example by weighing filtered seston from the control chamber) it is often calculated as volume per time without indication of how much seston that volume of water contained. Still, CR is more informative than filtration capacity with regard to bioremediation of waste as it gives the volume of water (or time spent clearing water) that is cleaned of seston after going through an individual per unit time rather than just the total amount of water passing through the individual.

There are several definitions in the literature causing filtration rate (FR) to be an unclear term. Widdows (1978) defined FR as the volume of water cleared of particles per unit time and this definition is similar to the definition of CR given by MacDonald et al. (2011) or the filtration capacity defined by Lindahl et al. (2005). Riisgård and Møhlenberg (1979) clarify that when there is no recirculation of water within *M. edulis* or in a laboratory aquarium, FR is equal to CR. They (Riisgård and Møhlenberg, 1979) measure FR as a volume per unit time and Melzner et al. (2011) follow suit. Hawkins et al. (1998) and MacDonald et al. (2011) measure FR as the amount of seston removed and display it as a weight per hour. This makes it difficult to compare measurements from different areas and studies (Table 1).

Another variable in filter feeding is the assimilation efficiency (AE). For this measure, the definitions are most similar across publications. AE is the percentage of organic matter taken up from the water column and is measured by comparing organic matter in the faeces to the organic matter in the diet (MacDonald et al. 2011). The majority of studies carried out on filtration in *M. edulis* have been undertaken in laboratories, often using single species of algal cells as food. Therefore they may not be very meaningful in the field, and disagreements between laboratory and field measurements have been found (Hawkins et al., 1996).

2.2 Primary influences on filter feeding rates of *M. edulis*

Filtration in *M. edulis* is influenced by water temperature and water viscosity, the type and the availability of food in the water column, the metabolic rate and the size of the individual mussels (Riisgård et al., 2011). While temperature affects metabolic rates (Widdows, 1978), reduced temperature also increases viscosity of the seawater which reduces the rate of ciliary action (Larsen and Riisgård, 2009). Ciliary activity is the movement of specialised cell organs within gills that create a water current allowing bivalves to feed. Larsen and Riisgård (2009) suggest after careful evaluation of the literature that increased viscosity due to lower temperature is solely responsible for reduced ciliary activity in *M. edulis*, rather than further underlying biological reasons such as reduced metabolic rates. For *M. edulis* from the Baltic Sea this decline of ciliary activity due to low temperatures led to a reduction in feeding rates of 35 % (temperature difference approximately 8°C) (Melzner et al., 2011). Contaminants may also influence the filter feeding rates of *M. edulis*. For example, toxic hydrocarbons act on them as narcotics leading to a depressed clearance rate and diminished scope for growth through loss of feeding opportunity (Widdows et al., 1995).

2.3. The role of *M. edulis* in BW

Once seston have been filtered from the water by *M. edulis*, they assimilate the particles, as described in section 2.1 and 2.2, and hence participate in BW, through three mechanisms (Table 2): firstly through cycling/detoxification. They use metabolic processes that change wastes into harmless or less toxic compounds. This reduces the damaging effects of such wastes on themselves and other species. For example, they can take up toxic wastes from incomplete combustion of fossil fuels such as polycyclic aromatic hydrocarbons, and metabolise them to a less toxic form (example below) (Baumard et al.1999). Secondly, *M. edulis* participate in BW through sequestration and subsequent storage. They use processes that sequester waste in such a way that it is no longer biologically available in the water column and does not exhibit toxicity, for example by storing toxins from phytoplankton in their tissues. However, in this case, toxicity does occur when *M. edulis* are consumed by other species including humans (Mebs, 1998). Thirdly, by aiding export through all the processes that transport wastes out of a system, this includes atmospheric, benthic and lateral export. They produce two solid filtration products: faeces and pseudofaeces which are important in benthic-pelagic cycling and burial. Faeces are materials that have passed through the digestive system from where nutrition has been extracted. These materials are stuck together by mucus during the passage through the digestive system. Pseudofaeces are made up of a collection of materials that are either selected because they are not food or because there is too much food in the water column (Riisgård et al., 2011). Above a certain threshold of food (cells ml^{-1}) both types of faeces can be produced simultaneously. *M. edulis* also use mucus to bind pseudofaeces together (Riisgård et al., 2011). Both types of faeces have a higher mass of particles than small particles of seston. This can change the way organic matter is then transported through the water column. If it is dense it may sink faster but if it is less dense it may remain in the water column and be available to other species for longer periods of time (Newell, 2004). Once *M. edulis* die or are ripped off their support by strong wind and wave action, they fall to the seafloor and, due to hydrodynamic processes, get buried in sediments. This way, contaminants stored in their tissues are also moved to the seafloor and buried. Additionally, they excrete nitrogen in form of NH_4^+ (70%), urea (13%) and 5-21% ammino-N via urine. This excreted nitrogen is bioavailable and can lead to renewed phytoplankton and microphytobenthos production (Burkholder and Shumway, 2011; Newell, 2004).

2.4 Types of waste that *M. edulis* bioremediate

Waste can be defined as "materials for which there is no immediate use and that may be discharged into the environment" (Hinga et al., 2015). *M. edulis* can take up wastes via two pathways: direct absorption of the compound in the water phase through the gills or indirectly through the digestive system when the compounds are solid (Baumard et al., 1999). The role of *M. edulis* in the bioremediation of each waste varies depending on the type of waste; hence representative examples of wastes and how *M. edulis* bioremediates these at current CO_2 levels are discussed in turn here. The processes and how *M. edulis* deal with each of the waste types are also summarised in Table 2.

2.4.1 Nutrients, phytoplankton and organic matter

Phytoplankton and organic matter are primary food sources of *M. edulis* which they then convert into biomass (Riisgård et al., 2011). Excess nutrient loading (eutrophication) due to an imbalance in the nitrogen cycle caused by, river run-off from agricultural activities leads to increased growth of phytoplankton and greening of the water column (Riebesell, 1989; Heip, 1995; Diaz, 2001, Diaz and Rosenberg, 2008). Coastal eutrophication is one of the biggest threats to marine ecosystems and their functioning, leading to hypoxic zones particularly in shallow bays and enclosed seas (Diaz and

Rosenberg, 2008). Globally, it is likely to increase further due to sustained human population growth and resource intensification (Rabalais et al., 2010). This accumulation of organic matter in the form of living and dead phytoplankton has far reaching ecosystem, and ecosystem service, consequences. The abundance of phytoplankton in surface waters leads to a reduction of light penetration and hence photosynthesis in deeper waters. Dying and dead phytoplankton is digested by microbes reducing dissolved oxygen in the water column which can lead to hypoxic and anoxic zones (Diaz and Rosenberg, 2008; Gooday et al., 2009; Rabalais et al., 2010; Broszeit et al., 2013). Therefore, *M. edulis* are important in reducing phytoplankton biomass and organic matter and thereby the negative effects of eutrophication on the marine environment.

2.4.2 Toxic products of phytoplankton

M. edulis can readily accumulate lipophilic organic compounds, for example toxins produced by phytoplankton. They are capable of accumulating substantial amounts of some of these toxins because they are not affected by them (Moroño et al., 2001). They also transform these compounds into less harmful products which they then egest (O'Driscoll et al., 2011).

2.4.3 Examples of derivatives of burnt fossil fuel

Polycyclic aromatic hydrocarbons (PAHs) are products of fossil fuel and organic matter combustion. They are highly toxic, carcinogenic and mutagenic to marine and terrestrial animals and humans (Samanta et al., 2002). In the water column, they are available for filter feeders such as *M. edulis*. A study carried out on concentrations of PAHs in *M. edulis* in the Baltic Sea revealed that *M. edulis* can biotransform some PAHs, for example the carcinogenic benzo[a]pyrene (B[a]P) into the less dangerous benzo[e]pyrene (B[e]P) which was shown in the ratio of B[a]P to B[e]P within the tissues of *M. edulis* (Baumard et al., 1999). However, primarily *M. edulis* accumulate PAHs in their tissues and this can reduce their filter capacity as well as their reproductive success (Eertman et al., 1995), effectively reducing their contribution to BW.

2.4.4 Metals

In a short experiment (24 hours), Brzozowska et al. (2012) measured the uptake of heavy metals (zinc, lead, nickel and chromium) in two size classes of *Mytilus* sp.. Their results indicated that they can selectively remove heavy metals from seawater, meaning they found less of a reduction of chromium than the other three metals tested. They also showed that smaller individuals are less capable of selectively absorbing metals than larger ones. This indicates that mussels develop the ability to select metals they can take up as an important mechanism to ensure enough trace metals are taken in for their metabolism (Brzozowska et al., 2012).

2.4.5 Microplastics

Microplastics (< 1mm) are ubiquitous in the marine environment occurring in the pelagic zone as well as in sediments and marine organisms (Thompson et al., 2004; Cole et al., 2014). Their impacts on marine ecosystems are still poorly understood but it has been demonstrated that marine invertebrates, including *M. edulis* can take them up via feeding (Thompson et al., 2004). In *M. edulis*, after digestion, these particles are either egested in faeces or remain within the individual. Depending on size, they can cross into the hemolymph, or be stored in the digestive tubules and gut cavity. These authors also showed that exposure to microplastics also increased energy consumption by 25% when compared to those not exposed to microplastic. Microplastics may also transport contaminants into exposed organisms as these accumulate onto the particles (Mato et al., 2001). Such contaminants can then be moved through the food chain to higher trophic levels (Van Cauwenberghe et al., 2015). This means that *M. edulis* can either remove plastics from the environment or if they egest them, that they will be contained within faeces and therefore more likely to sink to the seafloor where they may be stored long-term.

2.4.6 Nanoparticles

Nanoparticles are particles of size <100 nm and due to their small size they end up in waterways and ultimately in the marine environment. A study by Tedesco et al. (2010) showed that gold nanoparticles fed to *M. edulis* accumulated in the digestive gland, a smaller portion in the gills and none in the mantle tissue. This means that *M. edulis* remove nanoparticles from the system by accumulation. Yet, little is known about the effects of nanoparticles on the environment or their bioavailability and uptake, digestion and effects on organisms. Studies so far show that nanoparticles can cross and damage biological membranes and cause oxidative stress in metazoan cells. Nanoparticles are increasingly developed and used for a number of purposes such as medicine, cosmetics and technical equipment, leading to their increased abundance in the marine environment.

2.4.7 Drugs

Pharmaceuticals and their metabolites occur in coastal waters, one study carried out in Ireland found 80 pharmaceuticals and their metabolites in municipal sewage effluent (McEneff et al., 2014). They are bioavailable and can be taken up by *M. edulis*, and then either accumulate in their tissues or become metabolised (Celiz et al., 2009).

2.5. Use of *M. edulis* in the management of water quality

A number of studies have investigated the role of *M. edulis* in reducing excessive nutrient loads in coastal waters and to test the feasibility of using *M. edulis* in the management of this pollution. *M. edulis* do not feed on nutrients directly but on the phytoplankton biomass that can grow because of the nutrients in the water column. For example, Lindahl et al. (2005) tested the feasibility of using *M.*

edulis aquaculture as a way of reducing nitrogen waste (N) in the Eastern Skagerrak, Sweden and demonstrated improved water quality. This work was also coupled with market valuation for bivalves and evaluation of a N market as is being implemented in Sweden and Norway, following a model by the US (Lindahl et al., 2005). Reid et al. (2010) measured the assimilation efficiency of *M. edulis* in faeces plumes of salmon cages and found that if they are placed in the actual plume they are capable of using the organic carbon of the salmon faeces as well as excess feed coming from the cages. Gren et al. (2009) calculated the cost-effectiveness of using *M. edulis* farms to abate nutrients in the Baltic Sea. Their results indicate that this aquaculture, particularly if *M. edulis* can be sold for human consumption, can have positive effects on nutrient levels and be economically feasible too.

Models to assess carrying capacity of coastal ecosystems for *M. edulis* and other types of fish and shellfish aquaculture are well developed and widely used. For example, they can show how physical, hydrodynamic and biological parameters can differ within bays and how these differences are reflected in *M. edulis* tissue growth in aquaculture farms (Waite et al., 2005; Grant et al., 2008; Filgueira et al., 2012). Areas within a bay with low seston concentrations due to reduced water exchange produce less growth in *M. edulis* (Waite et al., 2005). Overstocking of *M. edulis* can also lead to reduced growth, as they will compete with each other for food. Additionally, their own input of nutrients in form of faeces and urine may lead to negative effects on enclosed systems such as bays (Reid et al., 2010). Negative effects are often localised to the aquaculture farm and can include low biological diversity with a prevalence of opportunistic species such as polychaetes *Capitellidae* sp. below the farms, build-up of faecal matter which then leads to anoxia and build-up of toxic hydrogen sulphide (Burkholder and Shumway, 2011). The models used to assess carrying capacity of coastal ecosystems for aquaculture can also be useful in assessing the effectiveness of *M. edulis* in abatement of pollution (Lindahl et al., 2005; Gren et al., 2009).

3. What are the key effects of OA on *M. edulis?*

The effects of OA on marine organisms can be studied either by laboratory or field experiments. Due to the variety of ways of expressing pH changes and CO_2 concentration within the studies, different units are cited in this section. The CO_2 concentration in experimental tanks can be measured and displayed in several ways, for example as parts per million (ppm) or measured gas pressure (atm/µatm). Laboratory experiments may both under- and overestimate reactions of species to OA, because of their relatively short duration compared to the longevity of the species studied. They often do not take adaptation and evolutionary mechanisms into account nor biological or other interactions (Harvey et al., 2014; Hilmi et al., 2013). Field experiments might provide more realistic scenarios than laboratory experiments but are technically difficult to carry out. Therefore there are only few experiments of OA effects on *M. edulis* in the field (for example, Thompsen et al. 2010: Melzner et al.

2011). Natural CO_2 vents in shallow marine areas can aid research into future high CO_2 environments, by providing areas of long-term streams of CO_2 and in that they are open to naturally occurring assemblages. However, they only affect small areas allowing species sensitive to high CO_2 concentrations to avoid such areas (Hilmi et al., 2013). For example, the bivalve *Mytilus galloprovincialis,* a species closely related to *M. edulis,* is not found near natural vent systems of the Italian island Ischia (Hall-Spencer et al., 2008; Hilmi et al., 2013). No experiments, however, have been carried out looking at the effect of OA on bioremediation of waste.

3.1. Evidence of effects of OA on physiological processes related to filtration in *M. edulis*

As stated in Section 2.2 of this article, the filtration capacity of *M. edulis* is influenced by the following physiological factors: metabolic rate and size of the individual. This section therefore concentrates on effects of OA on these physiological traits.

Only few studies measured metabolic rate under OA in *M. edulis*. Thomsen and Melzner (2010) demonstrate that metabolic rate under OA conditions first increased at a pH of 7.7, and then decreased at higher pH levels (while remaining above the metabolic rate in the control animals). It has been shown experimentally that *Mytilus edulis trossulus* from the southern Baltic Sea have a local adaptation to low pH values. Jakubowska and Normant (2015) exposed individuals of this species to gradually reducing pH of 8.1, 7.5 and 7.0 over 36 hours (12 hours at each pH level). No significant changes in resting metabolic rates were found in this study. Other studies have worked with closely related species. Navarro et al. (2013) exposed juvenile *M. chilensis* for 70 days to 380, 700 and 1200 ppm of pCO_2 with results showing a significant reduction in oxygen uptake indicating a metabolic depression. *M. coruscus* showed a significant reduction of respiration rate under OA conditions with pH of 7.7 and 7.3 as opposed to 8.1 in the control (Wang et al. 2015). Garilli et al. (2015) measured metabolic rates of two Mediterranean gastropod species (*Nassarius corniculus* and *Cyclope neritea*) near CO_2 vents in Italy. They found that high CO_2 conditions increased metabolic rates and suggested that the gastropods increase their metabolic rate to maintain internal pH. On the other hand, Gazeau et al. (2014) exposed *M. galloprovincialis* to pH changes of 7.7 for a period of 10 months and they found no significant reduction in respiration rates unless temperature was increased for the same amount of time.

Shell length correlates significantly with pumping rate of *M. edulis* (Jones et al. 1992) and size of individual organisms depends on their growth rate. Slower growth will therefore lower the capacity to filter feed by reducing biomass at any given point in time. For the purpose of this review we concentrate on two ways in which *M. edulis* grow: somatic growth which leads to an increase in soft tissue while shell growth is necessary to protect the soft tissues. To allow shell growth, animals must be able to calcify and this is metabolically costly under OA (Garilli et al. 2015). Previous OA events due to volcanic activity, for example in the Late Permian Extinction, led to smaller body sizes of many molluscan calcifiers, termed the 'Lilliput effect' (Garilli et al. 2015). Shell growth and calcification are not interchangeable because shell growth occurs when several layers of shell are produced of which some are calcified (Furuhashi et al. 2009). Several parameters for shell growth can be measured such as changes in length, mass, shell thickness or it was split into organic and inorganic growth as well as aragonite and calcite growth. Other parameters that are measured in OA experiments, such as calcification, excretion of NH_4, immune responses or internal pH were excluded from this review as it can be argued that they are not directly related to filtering capacity.

In a comprehensive meta-analysis, Kroeker et al. (2013) showed that molluscs (the study summarised results at phylum level) are negatively affected by a reduction in ocean pH of 0.5. They found a mean 17% reduction in growth in all mollusc studies they assessed.

All studies that measured parameters affected by OA relevant to BW in *M. edulis* were carried out in the laboratory. They lasted from 20 days to six months (Table 3). Most studies measured several parameters, but only those relevant to BW are listed in Table 3. The shortest experiment lasted 20 days and the authors used scenarios ranging from pH 8.14 to 7.5 (O'Donnell et al., 2013). They found no significant differences in shell volume growth among the nine treatment levels they used, possibly due to the short time-frame of the experiment. However, byssus thread attachment significantly deteriorated under high OA scenarios. Only one experiment looked at survival, using a pH range from 8.1 to 6.7. It lasted for 44 days and found reduced survival at pH 7.1 and reduced shell growth at pH 7.6 (Berge et al., 2006).

Melzner, Thomsen and colleagues carried out several experiments lasting between five weeks and two months (Thomsen et al., 2010; Thomsen and Melzner, 2010; Melzner et al., 2011; Thomsen et al., 2013). They found that shell growth can remain stable if sufficient food is available (Melzner et al., 2011) and that somatic growth is unaffected by low pH (Thomsen et al., 2010; Thomsen and Melzner, 2010). They also found that shell growth is suppressed from pH 7.14 (4000 µatm). In an experiment lasting 35 days using pH range of 8.01 to 7.19 Thomsen et al. (2013) found no differences in shell growth. However, they found a significant decrease of inorganic shell growth at a pH of 7.7 (1021 µatm). Keppel et al. (2015) compared growth under current pH conditions (pH 8.10) to growth in pH 7.94. After a 10 week exposure there was no effect on somatic growth while all shell growth parameters increased under lower pH. This could be due to the smaller decrease in pH treatment compared to other studies, but also because the animals were fed at higher than natural rates which may help them invest in shell growth.

The longest study on OA effects in *M. edulis* lasted six months with *M. edulis* exposed to four levels of pCO_2 (380, 550, 750 and 1000 µatm) (Fitzer et al. 2014). Growth was reduced in animals exposed to 750 µatm and above 1000 µatm. This growth was compensated for by increased protein metabolism (Fitzer et al., 2014).

In general, the studies are widely conclusive that OA leading to low pH scenarios will have negative effect on *M. edulis* in terms of growth and survival. Evidence on the impact of OA on metabolic rate is more scarce.

3.2 Effect of OA on phytoplankton

To understand the impact of OA on *M. edulis*, it is also important to understand how OA will affect their primary food source: phytoplankton. Phytoplankton form the base of the marine food web and are crucial for biogeochemical cycling. Their enormous diversity makes it impossible to study the effects of OA on all species. Yet, their responses to climate change, particularly OA can lead to bottom-up control of the ecosystem (Harvey et al., 2014). *M. edulis* feed most effectively on any particles with sizes > 6µm with a filtering capacity of 90%, while the capacity to filter particles < 1µm is reduced to 15% (Canesi et al., 2012). For example, Bricelj and Kuenstner (1989) found that in a brown tide of the small phytoplankton species *Aureococcus anophegefferens* (2-3 µm) the CR and FR of *M. edulis* were reduced due to the small size of the alga. Therefore it is important to understand how phytoplankton communities will change under OA. Some models suggest that OA may lead to a size reduction in phytoplankton, for example during some seasons in the North East Atlantic (Artioli et al., 2014). Additionally, pH changes the character of nutrients in the sea, for example iron, which is expected to lead to changes in phytoplankton species abundances and distribution (Shi et al., 2010). This change in phytoplankton species abundance and distribution will affect *M. edulis* and ultimately the remediation of nutrients. This may subsequently lead to an increased likelihood of hypoxic zones (Tagliabue et al., 2011; Turley and Gattuso, 2012).

4. How does OA affect BW of *M. edulis*?

As shown in Section 2, *M. edulis* contribute to BW in several ways. With their filtration efficiency, they aid removal of pollution and eutrophication to such an extent that *M. edulis* aquaculture is used as a management tool to clean up bays and coastal areas, and around fish aquaculture (Lindahl et al., 2005; Reid et al., 2010; MacDonald et al., 2011). Studies discussed in Section 3 show that *M. edulis* are negatively impacted by OA, because, for example, they show reduced growth under OA scenarios. Size is one crucial factor in the ability of *M. edulis* to filter feed (Jones et al. 1992), because a larger individual can filter more water. Reduced growth was also found for *M. galloprovincialis* under a 0.3 pH unit decrease for 10 months. Animals under decreased pH showed reduced shell weight and fresh weight growth (Gazeau et al. 2014). Research into the effect of OA on feeding physiology of mytiluds is scarce. However, Wang et al. (2015) measured several metabolic indicators under OA and increased temperatures in *M. coruscus*. While growth was not affected by reduced pH alone, increased temperature led to a reduction in growth. Navarro et al. (2013) exposed the closely related species

Mytilus chilensis for 70 days to three levels of pCO_2 (380, 750 and 1200 ppm). They measured clearance rate (CR) and assimilation efficiency (AE) weekly on *M. chilensis* and found that with time, in the highest pCO_2 treatment, they showed a significant decline in CR. Additionally, AE was significantly higher in the control than the higher CO_2 pressures. In the same study of *Mytilus chilensis,* Navarro et al. (2013) also calculated production under OA scenarios. In 750 ppm and 1200 ppm scenarios a typical Chilenean aquaculture farm with 10 000 ropes will produce 13% and 28% less *M. chilensis* biomass respectively than under current conditions. They also measured that in the 1200 ppm treatment, AE was reduced by 18%. Adding these values together for *M. chilensis*, a reduction in filtration capacity of 46% (28% reduction in biomass and 18% reduction in absorption efficiency) under the 1200 ppm scenario may occur. Though this is a rather crude method of estimating this reduction (as it does not account for non-linear changes to these estimates) there are no other estimates available in the literature.

One study tested if metal pollution on *M. edulis* under different OA scenarios changed their survival and other health parameters (Han et al., 2014). Curiously, the experiment was carried out in tap water mixed with calcium carbonate rather than seawater.

While the effect of OA on filtration parameters has not been studied directly in *M. edulis,* filter feeding depends not only on external factors such as temperature and food availability but also on the size of the individual *M. edulis*. Therefore, if *M. edulis* show reduced growth and higher mortality under OA, this will lead to a reduction of BW capacity of *M. edulis*. Additionally, if OA leads to a decrease biomass of *M. edulis* (around 40-50%) as modelled by Fernandes et al. (unpublished), this will have detrimental effects on their ability to contribute to BW locally.

5. Discussion and conclusion

The service of bioremediation of waste is supported by many different ecosystem processes, with *M. edulis* making an important contribution to these processes. This service is also dependent on the quantity and type of wastes that are present in the marine ecosystem in a particular place. It is not currently feasible to quantify the contribution that *M. edulis* makes to this service. However, this study shows that they participate in the bioremediation of many different types of organic and inorganic wastes. This study indicates that their capacity to do so may change under a scenario of increased OA. OA is predicted to cause negative changes to *M. edulis* in terms of their physiology, biomass and their ability to filter feed.

Increasing levels of OA have the potential to reduce the bioremediation capacity of *M. edulis*, which, combined with similar impacts on other filter feeding bivalves (e.g. other mytilud species), could result in increased occurrence of harmful algal blooms, fish kills, hypoxic zones and shellfishery and beach closures. Such a reduction in water quality will have knock-on negative effects on other ecosystem processes and services such as food provision and recreation and tourism. Coastal ecosystems and embayments will be particularly affected because their hydrodynamic forces are reduced, leading to longer residence times of polluted water in such areas (Kemp et al., 2009; Filgueira et al., 2012). This is of particular importance to human populations because coastal ecosystems provide the majority of marine ecosystem services (Worm et al., 2006).

The potential reduction of BW due to negative effects of OA on *M. edulis* will also have negative impacts on their use in coastal management. Their effectiveness at removing excess nutrients and feed from aquaculture sites could be considerably diminished. By implication, this could mean that aquaculture farms may need to be kept at smaller scales, particularly where water exchange is reduced such as in coastal bays. There is also a trade-off between the services of food provision and BW which may be aggravated by OA. A reduction in *M. edulis* biomass could result in less harvestable biomass of *M. edulis* for human food consumption, coupled with a reduction in the service of BW. It may be necessary to carefully regulate harvest and seeding for human consumption to preserve the service of BW. Consequently, it is not only important to cut down CO_2 emissions to avoid a reduction in BW through *M. edulis* (and other filter feeders) but also to lower the amount of wastes entering the marine system, particularly those resulting in eutrophication.

OA and other stressors

OA is not an isolated pressure on the marine environment but works in concert with other stressors particularly increased sea and air temperature, eutrophication and hypoxia (Hendriks et al., 2010; IPCC, 2014). Increased temperature reduces the thermal tolerance of marine species including *M. edulis* and may also reduce their filtration rate (Widdows, 1978). Extreme warming events, such as occurred in Europe in 2003, can have negative effects on *M. edulis* abundance such as the example of M. edulis die-off during a heatwave in France in 2003 mentioned above. Several studies discussed in this manuscript used the combined stressors of temperature and OA and their results indicate that pH is a more detrimental stressor if combined with warming waters than on its own. For example, Gazeau et al. (2014) exposed *M. galloprovincialis* to OA and increasing temperatures and showed that temperature alone or temperature and pH led to 100% mortality in experimental animals. In addition, if sea water temperatures warm as predicted, then low oxygen situations occur (Diaz and Rosenberg, 2008). This will affect *M. edulis* as they prefer high oxygen concentrations (Joschko et al., 2008). Several studies have also found reduced resistance to pathogens and diseases under OA in *M. edulis* (e.g. , Bibby et al. 2008; Ellis et al. 2015) and other bivalve species (Ivanina et al. 2014). Bibby et al. (2008) exposed *M. edulis* to four levels of pH and showed that after 32 days there was a significant reduction of phagocytic activity in the lower pH treatments. *M. edulis* hemolymph also showed reduced antibacterial action after 90 days of exposure to OA treatments. In this study, however, the authors found that upon exposure to the pathogenic bacterium *Vibrio tubiashii,* the antibacterial functions of *M. edulis* hemolymph were restored. This may indicate a physiological trade-off between low pH and bacterial exposure. As such, *M. edulis* will be vulnerable to multiple stressors in the future, many with the potential to reduce the bioremediation capacity of this key species.

Conclusions

This study has shown that *M. edulis* are important contributors to BW due to their capacity to take up different types of wastes. OA is expected to impact the contribution that *M. edulis* have to the service of BW by depressing the capacity of *M. edulis* for growth and filtration. This will have knock-on effects for other ecosystem services, such as food provision.. Further research aiming to quantify the BW carried out by *M. edulis* would be invaluable if the ecosystem service of BW is to be better understood. Additional studies into the effects of OA on the filtering capacity of *M. edulis* would also facilitate the making of quantitative predictions of the effect of OA on BW. Finally, reducing CO_2 emissions and thereby slowing OA and the negative effects on *M. edulis* are crucial, if society is to continue to rely on *M. edulis* to contribute to BW. A reduction in CO_2 would not only lead to a reduction in the negative effects of OA but also help to slow the rise of global temperatures and the increasing spread of hypoxia, two additional stressors that are also negatively affecting the provision of marine ecosystem services.

Table 1: Different types of filtration measurements taken from the literature. TPM = total particulate matter, OC = organic carbon, OCI = organic carbon ingested, a, b, c in the calculation of FR in Hawkins et al. 1998 are coefficients no further explained in the original manuscript.

Measure of filtration	Definition (as given in the paper)	Calculation given	Unit used	Result	Setting	Reference
Filtration capacity	Amount of water filtered in a given time	Not given	$mL\ min^{-1}$	33-50	Field	Lindahl et al. (2005)
Exhalant siphon area	Size of open exhalant siphon	Not given	mm^2	16-49	Field	MacDonald et al. (2011)
Clearance rate	Not defined	Not given	$mL\ min^{-1}$	33	Lab	MacDonald et al. (2011)
Clearance rate	Volume of water filtered completely free of particles per unit time	Not given	$Lh^{-1}\ g^{-1}$	2-12, depending on cell abundance	Lab	Bricelj and Kuenstner (1989)
Filtration rate (FR)	Volume of water cleared of particles per unit time	Not given	Lh^{-1}	FR dependent on food concentration, size of animal and temperature	Lab	Widdows (1978)
Filtration rate (FR)	Not defined	Not given	$mg\ h^{-1}$	2.5-6	Lab	MacDonald et al. (2011)
Filtration rate (FR)	Amount of water transported through the gills = pumping rate	Not given	$mL\ min^{-1}$	33.1-41	Lab	Riisgård and Møhlenberg (1979)
Filtration rate (FR)	Not defined	Not given	$mL\ min^{-1}$	9.6	Lab	Melzner et al. (2011)
Filtration rate (FR)	Not defined	$FR=a*TPM^b*OC^c$	$mg\ h^{-1}$	4.13*(±9.28)*TPM* 1.91(±0.34)*OC2.26 *(±1.43)	Field	Hawkins et al. (1998)
Assimilation efficiency	Percentage of organic matter taken up from the water column	Not given	%	91.64-92.36	Lab	Bricelj and Kuenstner (1989)
Assimilation efficiency	Not defined	Not given	%	24-38	Lab	MacDonald et al. (2011)

Measure of filtration	Definition (as given in the paper)	Calculation given	Unit used	Result	Setting	Reference
Assimilation efficiency	Percentage of total ingested dietary organic matter that is absorbed during passage through the digestive system	Not given	%	54	Field	Reid et al. (2010)
Assimilation efficiency	Percentage of total ingested dietary organic matter that is absorbed during passage through the digestive system	Not given	%	81-90	Lab	Reid et al. (2010)
Assimilation efficiency	Percentage of total ingested dietary organic matter that is absorbed during passage through the digestive system	Not given	%	1.15*(±0.03)-[0.149(±0.004) 3(1/OCI)]	Field	Hawkins et al. (1998)

Table 2: *M. edulis* contribute to BW in several ways, varying by waste and process.

Process	Process number (Figure 1)	Mechanism in mussel	Nutrients, phytoplankton and organic matter	Toxic phytoplankton	Derivatives of burnt fossil fuels	Metals	Microplastics	Nanoparticles	Drugs
Cycling	1	Growth	✓						
Cycling	1	Detoxification		Not always	✓				
Sequestration	2	Bioaccumulation		✓	✓	✓	✓	✓	✓
Export	3	Excretion through faeces, pseudo-faeces	✓	✓	✓		✓	✓	
Export	3	Excretion through urine	✓	?		✓			

Not always: during metabolisation, some toxins become more toxic rather than being detoxified.

Table 3: Effect of OA on *M. edulis* as demonstrated in experimental studies. Parts of the table are reproduced from Parker et al. (2013). Units of CO_2 and pH measurements are taken from each paper but cannot be standardised as insufficient information was provided to carry out conversion. Therefore they are not consistent within the table. Arrows up: a positive effect, arrows down: a negative effect, sideways arrows: no significant effect.

Experimental duration	Experimental treatment: CO_2/pH	Parameter measured	Impact	CO_2/pH level that first caused significant change	Author(s)
20 days	300, 500, 600, 800, 1000, 1100, 1200, 1300, 1500 µatm / 8.14-7.50	Shell volume growth	↔		O'Donnell et al. (2013)
35 days	472, 1021, 2114, 3350 µatm / 8.01, 7.7, 7.4, 7.19 and high or low food	Shell length growth	↔		Thomsen et al. (2013)
		Inorganic shell growth	↓	1021 µatm	
		Organic shell growth	↔		
44 days	NA / 8.1, 7.6, 7.4, 7.1, 6.7	Survival	↓	7.1	Berge et al. (2006)
		Shell growth	↓	7.6	
2 months	385, 1400, 4000 ppmv /8.05, 7.56, 7.08	Shell growth	↓	4000 ppmv	Thomsen et al. (2010)
		Somatic growth	↔		
2 months	385, 1120, 2400, 4000 µatm / 8.03, 7.7, 7.38, 7.14	Shell growth	↓	4000 µatm	Thomsen and Melzner (2010)
		Somatic growth	↔		
		Metabolic rate (oxygen consumption)	first ↑, then ↓	1120 µatm	
10 weeks	400, 760 ppm/ 8.10, 7.94 , also ambient temperature, plus 4 °C	Shell length growth	↑	760 ppm/7.94	Keppel et al. (2015)
		Whole animal wet	↑	760 ppm/7.94	

Experimental duration	Experimental treatment: CO_2/pH	Parameter measured	Impact	CO_2/pH level that first caused significant change	Author(s)
		mass			
		Total dry mass	↑	760 ppm/7.94	
		Calcified mass	↑	760 ppm/7.94	
		Soft tissue dry mass	↔		
		Calcified mass/soft tissue dry mass	↑	760 ppm/7.94 (in higher temperature)	
7 weeks	39, 142, 240, 405 Pa/NA, high or low food	Shell growth low food	↓	405 Pa	Melzner et al. (2011)
		Shell growth high food	↔		
6 months	380, 550, 750, 1000 µatm/NA and control temperatures or 2°C temperature increase	Shell growth	↓	550 and 750, but not at 1000 µatm	Fitzer et al. (2014)
		Calcite growth	↑	1000 µatm	
		Aragonite growth	↓	550 µatm	

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