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Linking the biological impacts of ocean acidification on oysters to changes in ecosystem services: A review

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Abstract: Continued anthropogenic carbon dioxide emissions are acidifying our oceans, and hydrogen ion concentrations in surface oceans are predicted to increase 150% by 2100. Ocean acidification (OA) is changing ocean carbonate chemistry, including causing rapid reductions in calcium carbonate availability with implications for many marine organisms, including biogenic reefs formed by oysters. The impacts of OA are marked. Adult oysters display both decreased growth and calcification rates, while larval oysters show stunted growth, developmental abnormalities, and increased mortality. These physiological impacts are affecting ecosystem functioning and the provision of ecosystem services by oyster reefs. Oysters are ecologically and economically important, providing a wide range of ecosystem services, such as improved water quality, coastlines protection, and food provision. OA has the potential to alter the delivery and the quality of the ecosystem services associated with oyster reefs, with significant ecological and economic losses. This review provides a summary of current knowledge of OA on oyster biology, but then links these impacts to potential changes to the provision of ecosystem services associated with healthy oyster reefs.

Keywords: climate change; shellfish; aquaculture; sustainability; ecosystem approach.

1. Introduction

The risks arising from climate change are now widely acknowledged as a major cause for concern, yet awareness of ocean acidification is far less prevalent (Gattuso et al., 2015). Consequently, our understanding of the scope and severity of ocean acidification (OA herein) and its impacts on the marine environment remain relatively limited, and especially, the implications of OA to the continued provision of valuable ecosystem services.

Since 1750, the oceans have absorbed approximately 30% of anthropogenic CO_2, altering oceanic carbonate chemistry by reducing carbonate ion concentrations (CO_3^{2-}), and reducing the saturation states of calcite and aragonite. The result – lower pH, or ‘ocean acidification’ (Gattuso et al., 2014). Historic OA linked to the Permian-Triassic mass extinction led to the disappearance of ~90% of marine species (Clarkson et al., 2015). Today, without significant cuts in CO_2 emissions, a 150% increase in the concentration of surface ocean H^+ is predicted by 2100 (Stocker et al., 2013).

OA may be of benefit to some organisms, such as jellyfish and toxic species of algae (Hall-Spencer and Allen, 2015; Uthicke et al., 2015), but for other species, such as corals and molluscs that use calcium carbonate in their structures, OA is expected and has been shown to cause considerable direct harm (Basso et al., 2015; Comeau et al., 2015; Gazeau et al., 2014; Houlbrèque et al., 2015; Kim et al., 2016; Milazzo et al., 2014; Sui et al., 2016; Tahil and Dy, 2016). It is therefore unsurprising that it is the negative effects of OA on individual organisms that have received the most attention in the literature to date (see reviews by Albright, 2011; Brander et al., 2012; Fabricius et al., 2014; Gazeau et al., 2013; Hoegh-Guldberg et al., 2007; Pandolfi et al., 2011; Parker et al., 2013). However, the ecosystem effects and loss of ecosystem services associated with OA remain conspicuously absent, despite the increased prevalence of ecosystem-based approaches in environmental legislation and management. Here, we address that gap and introduce the current state of knowledge required to underpin a multidisciplinary evaluation (Knights et al., 2014), that considers the ecological, social and economic consequences of OA.

We have focused our review on an important ecosystem engineer (*sensu* Jones et al., 1996) and commercially valuable species, the oyster, although much of the discussion will also be relevant to other reef forming species. Oysters provide a number of ecosystem services (ESs herein) to society, including the formation of extensive reef structures that not only improve water quality, but are also an important food source (see Section 3). Worldwide, oyster reefs have dramatically declined in the past century and are now at the centre of many conservation measures and restoration strategies (Beck et al., 2011; Grabowski and Peterson, 2007), but these efforts are being undermined by OA. A plethora of recent reviews and meta-analyses have highlighted the threat of OA to marine fauna (see references above), but are often restricted to the description of biological effects on a range of taxa, and do not focus on specific species or groups of organisms (but see Albright, 2011; Gazeau et al., 2013; Hoegh-Guldberg et al., 2007; Parker et al., 2013, for reviews on corals and shelled molluscs). To date, there have been no reviews focused on oysters, despite their ecological, economic and societal value.

This review is in two parts: firstly, we undertake a brief review of the biological and ecological impacts of OA on oysters. This includes an assessment of the effects of OA on individual life history stages (planktic larvae and sessile juveniles and adults), populations and ecosystem-level responses. We then review the range of ecosystem services that are provided by oysters, including an assessment of their economic value and associated metrics. We conclude by considering how impacts at the organismal-level can affect the provision of ecosystem services.

2. The biological impacts of ocean acidification on oysters

2.1. Effects of OA on reproduction and planktic life-history stages

The planktic larval stage is a crucial life-history stage for many benthic organisms and changes in development, performance or survival of this stage can critically influence juvenile-adult population dynamics and ecosystem functioning (Bachelet, 1990; Green et al., 2004; Rumrill, 1990). The early development stages of marine calcifiers were quickly identified as particularly vulnerable to OA, with the potential to alter population size and dynamics, and community structure (Kurihara, 2008). As such, there has been a burgeoning literature describing larval responses to OA (reviewed in Albright, 2011; Byrne, 2011; Przeslawski et al., 2014; Ross et al., 2011).

OA has been shown to induce narcotic effects on motile life-history stages, reducing fertilisation success (Byrne, 2011). In a number of instances, OA effects include reduced sperm motility, reductions in fertilisation success and hatching rates of embryos (Barros et al., 2013; Parker et al., 2009; Parker et al., 2010), although in the case of Parker et al. (2009), changes could not be solely attributed to OA due to the effects being conflated with suboptimal culture temperatures. However, OA-induced narcosis has not been consistently shown, with disparity between studies of the same species (e.g. Kurihara et al., 2007; Parker et al., 2012). Parker et al. (2012) suggest this disparity may be the result of intraspecific phenotypic plasticity, whereas Byrne (2011) argues that the fertilisation process in marine invertebrates can be resilient to fluctuations in pH and may not be a reliable end-point. Neither Parker et al. (2012) or Byrne’s (2011) theories have been tested, but the inconsistencies shown highlight the need for comparative studies using discrete populations to determine if OA has consistent and repeatable effects, irrespective of scale or location.

In contrast to the fertilisation process, embryos and larvae are considered less tolerant to the effects of OA (Kroeker et al., 2010; Parker et al., 2012), in part because molluscs and other calcareous shell-forming species commonly lack the specialised ion-regulatory epithelium used to maintain acid-base status (reviewed in Lannig et al., 2010). The process of shell mineralisation begins at the trochophore (prodissoconch I) stage (reviewed in Gazeau et al., 2013). Larvae use two types of calcium carbonate, firstly mineralising highly soluble amorphous calcium carbonate (ACC) (Brečević and Nielsen, 1989) before switching to aragonite (Weiner and Addadi, 2002; Weiss et al., 2002). In juvenile and adult stages, this again changes to the use of low solubility calcite instead (Lee et al., 2006; Stenzel, 1964). Because the calcium carbonate structures formed in these early life-history stages play a crucial role in protection, feeding, buoyancy and pH regulation, disruption of calcification from OA could have significant consequences for survival (Barros et al., 2013; Simkiss and Wilbur, 2012). In other taxa, OA has been shown to greatly alter the structure of the important larval shell of calcifying organisms, including affecting dissolution rates and causing shell malformation, stunted growth, altered mineral content, and weaker skeletons (reviewed in Byrne, 2011; and Kurihara, 2008).

OA can also affect development rates. Multi-stressor experiments manipulating $p\mathrm{CO}_2$, pH, total alkalinity, and Ω_{arag} in order to simulate future acidification scenarios have shown that oyster larvae are highly sensitive to predicted future conditions. Responses include lower survivorship, abnormal development, smaller body size, and altered shell properties (Gazeau et al., 2013; Guo et al., 2015; Hettinger et al., 2013a; Hettinger et al., 2012; Parker et al., 2009; Parker et al., 2013; Talmage and Gobler, 2009; Timmins-Schiffman et al., 2012; Watson et al., 2009). However, the response remains inconsistent, with differences between species and regions apparent (see Gazeau et al., 2011; Kurihara et al., 2007; Parker et al., 2010 for a regional comparison of *Crassostrea gigas* performance), with the differences within species suggestive of pre-adaptation determined by exposure in their respective natural environment (*sensu* environmental filtering, Kraft et al., 2015).

OA places individuals under stress as they try to regulate or maintain physiological function. Processes including shell mineralisation, maintenance of internal acid-base balance, somatic growth, swimming and feeding are energetically expensive (Pörtner et al., 2004), and require additional energy for maintenance under OA (Pörtner, 2008). As such, the planktic larval stage can be extended to allow individuals to compensate for inefficient feeding and delayed development, but doing so may subsequently affect the fitness, competitive ability and survivorship of the individual at later life-history stages (Anil et al., 2001; Gazeau et al., 2010; Rumrill, 1990; Talmage and Gobler, 2009). Trade-offs between calcification and other physiological aspects are expected to occur, but the extent to which these occur and their impact, will depend on an individuals’ ability to obtain sufficient energy from their environment to counteract any negative effects of acidification (Hettinger et al., 2013a).

2.2. Carry-over or latent effects: metamorphosis to juvenile-adult stages

Changes in larval fitness are expected to impact adult population success through a combination of latent/carry-over effects (see Pechenik, 2006) and bottleneck effects (Schneider et al., 2003). These effects may only be transient, for instance, in cases where larval development is slower and the increased risks associated with extended larval duration (e.g. mortality from predation, starvation) enhance bottleneck effects. However, if larval development is unchanged and larval duration does not vary, the full suite of consequences will be transferred to the juvenile (carry-over effects). Consequences may include reduced environmental tolerance, decreased predation resistance, and increased mortality, which can introduce an additional bottleneck for the adult population (see Gaylord et al., 2011).

The negative impacts of OA on both pre- and post-settlement processes in oysters are clear. These include: reduced metamorphosis success (Hettinger et al., 2013a); greater mortality of juveniles (Beniash et al., 2010; Dickinson et al., 2012); shell weakening (Dickinson et al., 2012) and greater prevalence of micro-fractures; a reduction in shell dry mass, soft-tissue mass (Beniash et al., 2010; Dickinson et al., 2012) and growth (Hettinger et al., 2013b; Hettinger et al., 2012; Parker et al., 2011).

Metamorphosis is a crucial step in population development and growth and mortality is often high due to the high energetic cost (Gosselin and Qian, 1997; Videla et al., 1998). OA can lead to the depletion of energy reserves (e.g. lipids), impair larval fitness and decrease the likelihood of successful metamorphosis by up to 30% (e.g. Talmage and Gobler, 2009). A delay in metamorphosis can reduce energy reserves and lead to settlement in suboptimal habitat, such that post-settlement competence is impaired and mortality rates increased (see the extensive work by Jan Pechenik, including Pechenik, 2006; Pechenik et al., 1998). Given that post-settlement mortality often exceeds 90% under natural environmental conditions (Thorson, 1950), any additional impact on juveniles fitness or survival associated with OA impacts is likely to lead to significant consequences in terms of adult population density.

It has been suggested that negative consequences of OA on juvenile and adult oysters are carried-over as a result of energetic deficits experienced during the early (planktonic) life stage (Hettinger et al., 2013b); a less fit larva will likely become a less fit (e.g. smaller) juvenile/adult (Hettinger et al., 2012). These consequences may, in general, be negative but individuals from specific regions or some species appear to have developed coping mechanisms. Ko et al. (2013) recently provided evidence of compensatory mechanisms in *C. gigas* juveniles raised under acidified conditions, in which individuals displayed more rapid calcification (without a reduction in shell thickness or change in microcrystalline structure). Parker et al. (2011) demonstrated that some bred populations of *Saccostrea glomerata* were more resistant to OA than wild populations. While both bred and wild-caught individuals displayed significant reduction in shell growth at pH 7.8, wild populations were more susceptible to OA conditions than the bred population. The authors argue that these differences could be due to phenotypic plasticity emanating from different parental history, and/or differences in enzymatic activity of carbonic anhydrase - an enzyme linked with acid-base regulation and shell formation. Irrespective of the mechanism(s) of resilience, some species may be better suited for future OA conditions, and identification of resilient lineages may provide important insights for future food biosecurity and decision-making (see part 3.3).

2.3 OA impacts on adult oysters

Early studies indicated adult oysters were relatively robust to OA, leading to the rapid focus on early life history stages. Negative responses of adults were largely overlooked (see review by Gazeau et al., 2013; Parker et al., 2013), despite evidence of reduced calcification and shell growth (Beniash et al., 2010; Gazeau et al., 2007; Parker et al., 2009; Ries et al., 2009; Waldbusser et al., 2011b; Wright et al., 2014), decreased shell density, weight, and strength (Bamber, 1990; Welladsen et al., 2010), increased shell dissolution (Waldbusser et al., 2011a), and increased mortality (Beniash et al., 2010; Dove and Sammut, 2007). Metabolic activities have also been shown to be impaired, but have received little attention to date, with additional studies needed. In the few studies available, a consistent response across species has been apparent, notably impaired feeding activity (Dove and Sammut, 2007). Impaired filtration and feeding has the potential to effect energy supply and metabolic maintenance in adult oysters, and may affect resilience and persistence to OA in the long term.

Lower pH has been shown to affect the immune response of several taxa (bivalves and echinoderms, Asplund et al., 2014; Beesley et al., 2008; Bibby et al., 2008; Dupont and Thorndyke, 2012; Matozzo et al., 2012), but not others (decapods, Small et al., 2010). In oysters, several studies have shown negative effects. Li et al. (2009) noted impediment to metabolic activities of *C. gigas* under food deprivation and extended recovery time post-spawning, which they linked to an impaired immunological response. Wang et al. (2016) recently demonstrated that reduced pH (≤7.8) negatively impacted the immune system of *C. gigas* by increasing haemocyte apoptosis and reactive oxygen species production, inhibiting the activity of antioxidant enzymes, and influencing the mRNA expression pattern of immune related genes.

In *Crassostrea virginica, Crassostrea angulata,* and *C. gigas*, suppression of immune-related functions including haemocyte production and antioxidant defence was compromised leading to greater sensitivity to metal pollutants (Ivanina et al., 2014; Moreira et al., 2016). Li et al. (2015) showed short-term OA and warming significantly altered immune parameters of the Pearl oyster, *Pinctada fucata*, impacting acid-base regulation capacity, immune system functioning and bio-mineralization. Altered immune functions of bivalves from acidification can potentially lead to higher susceptibility to pathogens (Asplund et al., 2014; Beesley et al., 2008; Bibby et al., 2008; Ellis, 2013). For example, *Vibrio tubiashii*, a well-known pathogen of oysters that causes significant losses to the aquaculture sector (Dorfmeier, 2012; Elston et al., 2008; Richards et al., 2015a) grew more quickly, increasing the likelihood of outbreaks, although the susceptibility of the oysters to pathogens did not change.

2.4 From individual to ecosystem-level effects: consequences for the oyster reef

It is apparent that oysters, like many other marine invertebrates, are vulnerable to OA, yet consequences at the population and ecosystem level remain largely unknown. Many of the effects of OA are non-lethal, but substantial ecosystem changes can be expected as systems become restructured, with ‘winners’ and ‘losers’, through environmental filtering and niche partitioning (Barry et al., 2011; Fulton, 2011; Kraft et al., 2015; Somero, 2010). Such changes have already been seen in other taxa based on laboratory, mesocosm and field-based experiments, which all show that acidification favours some species, such as macroalgae and invasive invertebrates (Hall-Spencer and Allen, 2015), over others (Brodie et al., 2014). Ecosystem changes can be dramatic. For example, Christen et al. (2013) observed a phase shift from a calcareous-dominated system to one dominated by non-calcareous species. In Australia, the introduced Pacific oyster, *C. gigas*, is more resilient to acidification than the native *S. glomerata* (Parker et al., 2010) and may dominate interactions in the future. Should there be a shift in dominance toward the non-native species, the question remains as to whether *C. gigas* can provide functional redundancy and continue to provide the suite of ESs currently derived from *S. glomerata* or be lost altogether?

OA may affect community composition by altering interspecific interactions, between different trophic levels. For oysters, OA is predicted to lead to greater vulnerability to predation due to the negative effects on shell dissolution and microstructure (see references above). In some instances, the predator themselves may also be affected. For example, Sanford et al. (2014) found that *Urosalpinx cinerea*, a major gastropod predator of *Ostrea lurida*, consumed significantly more oysters in acidified treatments than in control treatments. Suggested reasons for this were reduced energetic value of the prey species, reduced prey handling time, increased energetic requirements of the predator or a combination of these (Kroeker et al., 2014).

Sites with naturally acidified conditions, such as volcanic seeps, lagoons and upwelling areas, can provide insights into long-term community responses to OA, particularly in areas subjected to anthropogenic stress (see studies by Basso et al., 2015; Range et al., 2012; Thomsen et al., 2012; Thomsen et al., 2010; Tunnicliffe et al., 2009). Field studies of mussel and vermetid reefs have shown that, in oligotrophic conditions, reduced pH levels benefit non-calcified algae, but impairs mollusc larval recruitment and dissolves carbonate habitat (Cigliano et al., 2010; Comeau et al., 2015; Kroeker et al., 2012; Milazzo et al., 2014; Rodolfo-Metalpa et al., 2011). Studies of the impacts of shallow-water oyster reef degradation show that loss or damage to these habitats can trigger cascading effects, including loss of biodiversity, reductions in biofiltration, and loss of coastal habitat protection (Rossoll et al., 2012).

2.5 Potential for adaptation

There are concerns over whether species will be able to adapt to the current unprecedented rates of environmental change (Somero, 2010; Sunday et al., 2014; Visser, 2008). Fast-generating species such as the pond algae, *Chlamydomonas,* did not show evidence of adaptation to acidified conditions after 1000 generations (Collins and Bell, 2004), although recently, the marine polychaete, *Ophryotrocha labronica*, demonstrated acclimation after just two generations (Rodríguez-Romero et al., 2015) indicating vastly different propensity for adaptation. It might be reasonable to assume that long-lived, slow generation time species, such as oysters, are even less likely to evolve rapidly (Barry et al., 2011; Byrne, 2011). However, Parker et al. (2015; 2012) demonstrated conferred tolerance from adults exposed to elevated CO_2 to their offspring (also dependent on if the oysters originated from wild or aquaculture-reared populations), suggesting hereditary traits as a mechanism of resilience. But as in fast generation time species, the potential for adaptation may be species-specific, as well as dependent on the heritage of the individual (Parker et al., 2010; Parker et al., 2011 respectively; Thompson et al., 2015).

A possible mechanism through which resilience to environmental stress can be achieved may be linked to the ‘quality’ of the environment. In the Baltic Sea, seasonal upwelling of eutrophic water leads to very high CO_2 levels and phytoplankton blooms, nevertheless, blue mussel reefs are able maintain their structure and function. Thomsen et al. (2012) argued that the high food supply allows the mussels to offset the metabolic costs of hypercapnia (Thomsen et al., 2012); a hypothesis that would support why aquaculture-reared individuals may be more tolerant to OA than wild individuals. However, what is not yet clear is the extent to which resilience and survival is achieved at the expense of ES provision?

3. The impacts of ocean acidification on oyster-reef ecosystem services

3.1 Using ESs to assess the impacts of OA

3.1.1 Assessing and valuing ESs

ESs allow society to evaluate and estimate the social and economic impacts of changes in resource availability (Beaumont et al., 2007; Cooley, 2012). They provide a tangible link between ecosystem health and human use (Figure 1) that help to inform decision-making of how to sustainably use and protect ecosystems (e.g. deciding whether to provide financial incentives, Knights et al., 2014). This is especially important as human well-being is linked to the sustained provision of resources including food, fuel, shelter, and water (Díaz et al., 2006). However, clear context and definition of ESs is critical to their perceived ‘value’ (Friedrich et al., 2015).

There are a number of ways to value ESs. The most obvious - ‘*monetary value’* - can be useful in conjunction with frameworks, such as the *Total Economic Valuation* (TEV) framework, which provides a classification of the different types of economic values associated with ESs (DEFRA, 2013; Herbert et al., 2012). In TEV, ESs are classified as either ‘use values’ (those derived from human interactions with a particular resource) or ‘non-use values’ (derived solely from the knowledge that the resource exists currently and will continue to exist in the future (Figure 2)).

3.1.2 Valuing oyster-derived ESs

The value of a service can be relatively easily estimated when a particular ES has a market price. For example, in 2009, Pacific oysters bought for the food industry were valued at £1,815/tonne (Herbert et al., 2012). Other services, such as carbon sequestration (carbon credit values), or raw materials (shell cultch) can be valued in a similar way. But when no market price exists or the ES value is subjective, estimating value can be a difficult task. In these instances, approaches such as ‘Willingness-to-Pay’ (WTP. e.g.De Groot et al., 2002; Fletcher et al., 2014) can provide a ‘value’ based on what people are willing to pay to avoid or counteract the adverse effects of the loss of the ES. The WTP approach is less precise than using market values, but can still be used to infer ecosystem or ES value.

3.1.3 ESs and OA

Future OA conditions are predicted to negatively affect the availability and quality of ESs through direct or indirect effects on species and the ecosystem (Frommel et al., 2012) with major social and economic consequences (Figure 3) (Cooley et al., 2009). Studies have typically focused on particular habitats, such as coral reefs (Brander et al., 2012), locations of significant value (Bosello et al., 2015; Hilmi et al., 2014; Lacoue-Labarthe et al., 2016; Rodrigues et al., 2013), or an economic sector (Cooley and Doney, 2009; Moore, 2011; Narita and Rehdanz, 2016; Narita et al., 2012). Although an increasing number of studies have tried to quantify the economic implications of OA on ES provision (Brander et al., 2012; Cooley and Doney, 2009; Moore, 2011; Narita et al., 2012), they are often qualitative in nature due to a lack of quantitative data (Cooley, 2012; Hilmi et al., 2014; Hilmi et al., 2013). While qualitative assessments are valuable for indicating directionality of change in ES provision, it is challenging to include the findings in management decisions and investment prioritization without clear quantitative estimates of change. Therefore, future studies providing more quantitative estimates are critically needed in order to bridge those gaps.

3.2 Oyster-reefs ESs, their value, and impacts of OA

3.2.1 Oyster reef ecosystem services

Biogenic reefs provide a wide range of ecosystem services including supporting, provisioning, regulating, and cultural services (MEA, 2005; Teagle et al. this issue) (Figure 1). Oysters are ecosystem engineers (Jones et al., 1996; Jones et al., 1997), in that they form biogenic reefs providing habitat for a range of other species and contribute a number of ecosystem functions and services (Fletcher et al., 2012; Herbert et al., 2012) (Figure 4, Table 1). Importantly, oysters are both allogenic and autogenic engineers, and ESs originate from both individual oysters and the wider reef structure (Walles et al., 2015).

Allogenic ESs include water filtration, benthic-pelagic coupling, nutrient cycling, carbon sequestration, and food provision (from oyster harvesting), while autogenic ESs include habitat formation, food provision, erosion protection and shoreline stabilization (Figure 4, Table 1). Additionally, cultural services associated with oyster reefs include recreational harvesting, educational use (research) and cultural heritage (Paolisso and Dery, 2010; Scyphers et al., 2014).

The perceived and relative importance of oyster-derived ESs is context-specific (Scyphers et al., 2014). Local or regional characteristics, such as environmental conditions, but also local economy and communities, can influence the significance of each service, but also their susceptibility to OA. For instance, biofiltration is a particularly valued ES in areas that are: polluted or susceptible to eutrophication; intensely used for recreation; or located near to seagrass beds (Cerco and Noel, 2007). Alternatively, shoreline stabilisation and protection from erosion by oysters is of importance in coastal areas under threat of climate change and extreme weather events (Brumbaugh et al., 2010; La Peyre et al., 2014), and in other areas, seafood is considered most important (Cooley et al., 2012).

Determining the importance of ESs to society and the economy can be achieved using one of the valuation methods described in brief above. Several studies have estimated the value of ESs association with oyster reefs (Beseres-Pollack et al., 2013; Grabowski et al., 2012; Grabowski and Peterson, 2007; Henderson and O’Neil, 2003; Kroeger, 2012; Volety et al., 2014) but estimates are wide-ranging (e.g. Grabowski et al. (2012) valued oyster reefs at between \$5500-\$99000 ha^{-1} yr^{-1}, excluding the economic value from harvesting). Given local/regional priorities may vary, such varied estimates are unsurprising, but makes predicting the economic impact of OA on oyster reefs challenging and perhaps explains why no study has attempted to do so to date. In lieu of such an analysis, studies that estimate the economic losses emanating from damaged oyster reefs may be a useful proxy. Here, we use these studies to provide a first assessment of OA impacts on ES provision from oyster reefs. While it can be argued that drawing conclusions on the effects of OA from damaged reefs is unrealistic or inaccurate, it has the merit to reinforce the high value of oyster reef ESs, allow an initial estimate of losses to be undertaken, and provides direction for future studies.

3.2.2 Current state of oyster reefs

Despite the numerous ESs provided by healthy oyster reefs, reef conservation and health is rarely considered unless populations are in danger of collapsing or are threatened (Kirby, 2004). It is only in these instances that the value of oyster reefs is assessed; the outcomes used to direct restoration efforts (Beck et al., 2011; Coen et al., 2007; Grabowski et al., 2012; Grabowski and Peterson, 2007; La Peyre et al., 2014; Volety et al., 2014). A recent study estimated that 85% of native oyster reefs had been lost globally and that in many bays and ecoregions, reefs were less than 10% of their historical abundance and ‘functionally extinct’ (Beck et al., 2011). As such, there is an urgent need for an assessment of ESs provided by oyster reefs.

There is, however, on-going debate over what is considered an acceptable level of ‘ecological health’ for oyster reefs (Alleway and Connell, 2015). While it is recognised that reef degradation can lead to a decrease in, or even loss of, provision of many ESs (Coen et al., 2007; Table 1; Jackson et al., 2001; Paerl et al., 1998; zu Ermgassen et al., 2013), the impact of OA on ESs derived from oyster reefs is less clear. In fact, the potential consequences of OA are largely speculative, and based either on the physiological and ecological impacts observed during laboratory experiments, or using *in situ* field experiments in naturally acidified sites (see Section 2.4). These studies suggest that population sizes may decrease below the minimum threshold required for the desired level of ESs (Figure 4) and indicate an overall negative effect of OA on oysters’ early life stages, with direct consequences on juvenile and adult physiology as well as recruitment and population dynamics (see discussion in Section 2.4). However, while there have been studies examining the effects of OA on filtration rates, growth, and survival of oysters, there has been no attempt to date to link those effects to ES provision.

3.2.3 Ecosystem services associated with oyster reefs

Oyster reefs provide a number of important provisioning, regulating, habitat and cultural ESs (Table 1). Below we describe each of the ESs in turn, grouped using the MEA (MEA, 2005) and more recent ODEMM assessment (White et al., 2013), and consider how OA is likely to affect the provision of those services in the future.

3.2.3.1 Habitat/Structural Services

Oysters create large complex 3-dimensional structures (Knights and Walters, 2010), providing a unique habitat for many organisms, assuring life-cycle maintenance, and securing a diverse gene pool (Table 1). The maintenance of the reef structure relies notably on the successful recruitment of oyster larvae and juveniles into the adult population. By creating a mismatch between environmental conditions and larval/juvenile performance (see Section 2), OA can have direct negative impacts on the formation and replenishment of the reef structure (Table 1). Moreover, it can hold further negative consequences for the reef, by lowering gene pool diversity and creating additional bottlenecks. OA-induced reef deterioration is likely to alter the available niches for other species, and restructure the overall habitat, which can hold critical consequences for the provision of other ESs.

3.2.3.2 Provisioning Services

Biodiversity and Seafood (other than oysters)

Biogenic reefs are important to food webs and fisheries (Peterson and Lipcius, 2003) and many organisms use reefs as refugia from predators, as nests, or feeding grounds. Oyster reefs create critical habitat for a number of species, including other economically important molluscs, crustaceans, and various species of fish (reviewed in Coen et al., 2007; Coen et al., 1999; La Peyre et al., 2014; Scyphers et al., 2011; Tolley and Volety, 2005; Volety et al., 2014). In a recent analysis, Grabowski et al. (2012) estimated that one ha. of healthy oyster reef increases biodiversity and enhances commercial fish value by up to ~$4123 yr^{-1} (see also Grabowski and Peterson, 2007; Table 1), although that value-added benefit may only be apparent when the oyster reef is not located near to other biogenic habitats that provides a similar function (Geraldi et al., 2009). The value of oyster reefs can be used to justify a management action (Knights et al., 2014), for example, the decision to restore an oyster reef following degradation (an effective method for increasing fish and large crustaceans production, Peterson et al., 2003). At the time of writing, there is no indication or means of disentangling the 'value' of oyster reefs to biodiversity and seafood in differing states of health, nor a clear understanding of the likely state of oyster reefs under OA beyond an expectation that some reefs will be more susceptible to damage and lead to a reduction in ES provision. Current research is on going to determine if other/non-native species, appearing more robust to OA, can provide redundancy for the loss of biogenic reef species threatened by OA.

Ornamental and raw materials

Oyster shell is valuable to a number of sectors (Yao et al., 2014), including construction, agriculture, and wastewater treatment. The cost of oyster cultch is relatively low (~$126/tonne, Kwon et al., 2004; Table 1) and the calcium carbonate from the shells is used as grit for the rearing of poultry (Çath et al., 2012; Scott et al., 1971); as a construction material and substitute for aggregate in concrete or mortar (Yang et al., 2010; Yang et al., 2005; Yoon et al., 2003; Yoon, 2004); as a liming material and soil stabilizer (Lee et al., 2008; Ok et al., 2010); and to treat discharged wastewaters to remove phosphates and traces of toxic heavy metals such as cadmium, copper and nickel (Hsu, 2009; Kwon et al., 2004). As shell dissolution rates increase with OA, the availability of oyster shell for use as a raw material may decline in the future (in terms of abundance and/or ‘quality’), increasing the cost of the material to industry and raising the cost to the consumer.

The use of oysters for ornamental purposes has decreased in modern times, but there are historical references of the use of oyster shells as raw material for the creation of glass (Wedepohl and Baumann, 2000). Shells are still available commercially, with values ranging from £5-15 a shell (Lemasson et al. *unpublished*). OA is likely to impact on the provision of raw materials, by negatively impacting on the calcification process of oysters, promoting adult shell dissolution, and may well reduce the value of shells as a raw material. The economic costs that would be incurred because of the loss of this service are unclear, and no estimates are found in the literature to date.

3.2.3.3 Regulating Services

Climate regulation and carbon sequestration

A number of studies have suggested that oysters provide climate change mitigation as a result of carbon sequestration during the calcification process (Dehon, 2010; Grabowski and Peterson, 2007; Lee et al., 2010; Peterson and Lipcius, 2003; Wingard and Lorenz, 2014). Although it can be argued that oysters are net CO_2 producers on their own, this service is particularly valid when oysters are present in association with algae (Hall et al., 2011). While the calcification process in oysters has been extensively researched, the extent to which climate can be mitigated is not easily quantifiable, and the impact on the carbon cycle not easily determined (Hickey, 2008). Under OA, shell calcification is negatively affected as shell dissolution increases (Welladsen et al., 2010) as a result of corrosive waters. The carbon sequestration process and efficiency of the climate regulation service is therefore at risk. At the time of writing, there was no data assessing the value of such service, although estimates could be derived from the price of carbon credits, or be related to bequest value of the bio-sequestration of CO_2 (Herbert et al., 2012).

Disturbance prevention and coastal erosion protection

The 3-dimensional structure of oyster reefs provides protection from erosion and stabilising shorelines. Adjacent critical habitats, such as seagrass beds or saltmarshes, positively benefit from the attenuation of wave action and the modification of the local water flow (Coen et al., 2007; Scyphers et al., 2011). It is argued that shore stabilisation and erosion protection are the most valuable ESs provided by oyster reefs (Grabowski et al., 2012). How OA will affect the maintenance of the 3-dimensional reef structure is unclear (see also provisioning services above), but the impacts on early life history, juvenile and adult forms (discussed in Section 2) are predicted to lead to a reduction in reef size, and therefore, a reduction or loss of coastal protection and shoreline stabilisation properties. The ‘value’ of this ES is likely to continue to erode under climate change as the number and intensity of extreme weather events increases, such that the ability of reefs to attenuate wave action may be reduced (Michener et al., 1997).

The cost of using engineered shoreline stabilization solutions as an alternative to reefs can provide some insights into the value of this ES (termed ‘avoidance costs’), but as Grabowski et al. (2012) points out, this value is context-specific and highly dependent on factors including the location, infrastructure types and prices, local economy, and the level of exposure. Nevertheless, costs of coastal defence structures can be in the a few dollars to millions of dollars depending on the setting and requirements (Table 1, see Firth et al., 2014 for a review)

Water treatment and quality

Oysters are important bio-filters that improve water quality (Grizzle et al., 2008; Hoellein et al., 2015; La Peyre et al., 2014; Nelson et al., 2004; Newell, 2004) and affect nutrient cycling (Beseres-Pollack et al., 2013; Coen et al., 2007; Hoellein et al., 2015; Kellogg et al., 2013; Newell et al., 2005; Piehler and Smyth, 2011). A number of approaches have been used to attribute value to this ES. Grabowski et al. (2012) used nitrogen permits as a proxy for market price, estimating that one ha. of oyster reef removed a quantity of nitrogen valued to \$1385-\$6716 yr^{-1}. Beseres-Pollack et al. (2013) used the costs of adding a biological nutrient removal system to a wastewater treatment plant, valuing the nitrogen removal service at \$293,993 yr^{-1} in the Mission-Aransas Estuary (NB this is equivalent to between 44 and 212 hectares of oyster reef based on Grabowski et al., 2012 estimates). Oyster-mediated nitrogen removal was valued at \$314,836 yr^{-1} in the Choptank estuary, using an average monetary value of ~\$24 kg^{-1} of nitrogen removed specifically applied to their study site (Newell et al., 2005), \$18,136 per million oysters in Chesapeake Bay (Kasperski and Wieland, 2009), and \$3000 ac^{-1} yr^{-1} in Bogue Sound, using values derived from the North Carolina nutrient offset trading program of \$13 per kg of nitrogen removed (Piehler and Smyth, 2011). These values are, however, difficult to compare as they are based on multiple assumptions of what constitutes 'value' and the bodies of water are of different sizes and properties, but nevertheless highlight the important economic value of this ecosystem service provided by oyster reefs.

The continued provision of this ES has important indirect benefits to other ES provision that are often not considered. For example, improved water quality affects the provision of ESs by other healthy and functioning species and habitats, such as economically important seagrass beds (Cerco and Noel, 2007; Coen et al., 2007; Dennison et al., 1993; Grabowski et al., 2012; Kahn and Kemp, 1985; Meyer et al., 1997). Increased seagrass bed coverage that comes with improved water quality can also be incorporated into the economic valuation of oyster reefs. Grabowski et al. (2012) estimated that one ha. of oyster reef promoted 0.005 hectares of additional seagrass bed, valued at \$2584 ha^{-1}. Therefore, under OA, further economic losses can originate from adversely impacted adjacent habitats.

3.2.3.4 Cultural Services

Recreation and leisure

Improved water quality associated with health oyster reefs increases human well-being by reducing the likelihood of eutrophication (Lipton, 2004), and increasing recreational use of the environment. The value of recreation and tourism can therefore be used as an indirect estimate of the value of oyster reefs. Oyster reefs are socially recognised as a valuable resource; the U.S. National Research Council (2004) valued reefs using willingness-to-pay estimates at ~$222 million (Grabowski and Peterson, 2007; see also Volety et al., 2014). Reduced bio-filtration rates under OA will likely lead to increased eutrophication and reduced water quality, diminishing public appeal and generating financial losses from lower recreational use.

Spiritual experience and cultural heritage

Oysters hold a significant place in local culture, traditions and history. Many countries have a long history of oyster harvest and consumption (Kirby, 2004), including the USA (Dyer and Leard, 1994), France (Heral, 1989), and the UK (Humphreys et al., 2014; Mac Con Iomaire, 2006), which is celebrated during oyster festivals, such as the ‘Bluff Oyster’ in New Zealand (Panelli et al., 2008; Rusher, 2003), ‘Oysterfest’ in Australia (Lee and Arcodia, 2011), and the ‘Whitstable Oyster Festival’ and the ‘Falmouth Oyster Festival’ in the UK. Traditional oyster harvesting can be an important part of the local economy and creates a sense of community and heritage, with the desire for this activity to be sustainable and prosper (Dyer and Leard, 1994; Paolisso and Dery, 2010; Scyphers et al., 2014). The impact of OA on the provision of cultural services is difficult to assess, but a reduction in the persistence of oyster reefs (and the number of harvestable oysters) will likely impact on the sense of heritage and affect local economies and communities that rely on a long tradition of oyster harvesting. In the worst case, OA could lead to the disappearance of oyster festivals, leading to the loss of sense of tradition and community well-being, as well as negative economic impacts locally through reductions of tourism.

3.3 Economic Impacts of OA on oyster harvest and aquaculture

The vulnerability of shellfisheries to OA and the likely economic consequences is of growing concern (Ekstrom et al., 2015; Haigh et al., 2015; Seijo et al., 2016). Although the 'value' of reefs is highly variable and context-dependent in terms of harvest yield, OA is likely to negatively affect the resilience, persistence, and sustainable use of wild oyster reefs into the future. In response, wild harvests now represent only a small proportion of oyster production worldwide, and increasingly replaced by aquaculture (130,754 tonnes of wild harvest compared to 5,155,257 tonnes of aquaculture production; valued at $ 4,174,258,000 in 2014 - FAO data[1]).

Aquaculture is the fastest growing food sector, and production reached an all-time high of 90.4 million tonnes in 2012 (FAO, 2014). In the UK, the decline of the native oyster, *O. edulis*, led to the introduction of the Pacific oyster, *C. gigas*, which now represents over 90% of the country's oyster production (Humphreys et al., 2014). Approximately 1200 tonnes of Pacific oysters are estimated to be produced each year in the UK (Herbert et al., 2012) worth an estimated £10.14 million (Humphreys et al., 2014). Given the demand and value of shellfish

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[1] http://www.fao.org/fishery/statistics

aquaculture, determining how OA will affect food security in the future is a crucial question that remains unanswered, although in 2010, the United Nations Environment Programme (UNEP) cited OA as a major threat to food security (UNEP, 2010). At locations where the effects of OA are already being felt, damages to the oyster aquaculture industry have been disastrous. In the US, the Pacific North-west region hosts an oyster industry worth over $72 million, but since 2007, several oyster hatcheries have suffered from mass mortalities of oyster larvae of up to 70-80% due to the upwelling of waters that were acidified, highly saline and rich in *V. tubiashii* (Barton et al., 2015; Elston et al., 2008; Feely et al., 2008). Similar impacts are expected in UK shellfisheries and elsewhere under combined scenarios of acidification and warming (Callaway et al., 2012).

Concerns have been expressed regarding the likely imbalance in the social and economic consequences of OA experienced by different communities (Ciuriak, 2012; Cooley et al., 2012). Islands and coastal communities that rely heavily on seafood as a source of protein and for their livelihood (e.g. tourism), are expected to suffer most, particularly as their potential for adaptation and mitigation is restricted due to lower financial means and limited access to technologies (Cooley et al., 2009; Hilmi et al., 2014; Hilmi et al., 2013; UNEP, 2010). Seafood aquaculture holds the potential to provide food security in a future where growing population and growing income are expected to increase the demand for food. However, for aquaculture to be sustainable, there is a need to recognise that the sector is nested in a sensitive system interconnecting economic, social and ecological spheres, whereby impacts on one sphere will likely disrupt the others (Bailey, 2008; Schmitt and Brugere, 2013; Soto et al., 2008).

Some argue that shellfish aquaculture will be impacted less by OA than wild harvests (Rodrigues et al., 2013), for instance, the rearing of larval stages in tanks may mitigate the impacts of OA. Further, the use of informed 'climate-proof' management measures, designed to buffer the effect(s) of OA, such as quality control and close monitoring of water quality may minimise any potential effects (Hilmi et al., 2014; see also the case study on the mitigation of the effects of ocean acidification on prawn and scallop fisheries in Australia by Richards et al., 2015b). In the Pacific North-west, oyster hatcheries have benefitted from close monitoring of seawater quality, which has greatly improved yield and reduced mortality (Barton et al., 2015). Relocation of hatcheries and farms to areas of higher water quality and environmental conditions more suited to the rearing of larvae is an option already considered by shellfish producers (Barton et al., 2015), although this may represent a costly alternative. Aquaculture farms could focus on more resistant species, such as *C. virginica* and *C. gigas* (Gobler and Talmage, 2014; Guo et al., 2015; Parker et al., 2010), and hatcheries could select for lines that produce the highest survival rates, such as selectively bred lines (Parker et al., 2011; Thompson et al., 2015). However, such scenarios must rely on robust scientific knowledge of the response of the different life stages of different species of oysters to OA. Moore (2011) claims that damage to individuals, and especially their shell, which appear to be susceptible to low pH (Welladsen et al., 2010), are unlikely to hold significant economic impacts as long as the organism survives the culture process. However, OA has the potential to impact on the final quality and value of the product by affecting the wet tissue mass, the shell appearance (due to corrosive waters), tissue texture and taste (Dupont et al., 2014), and potentially their nutritional value.

OA is likely to increase production costs due to the necessary buffering measures taken during husbandry procedures, such as pH and Ω_{ar} manipulations and increased feeding, as well as the costs associated with the longer developmental time of the early life stages, unless the production is focused on OA-resistant species or lines. New models should be investigated in order to link future levels of OA with variations in the production of oysters, and to try and predict to what extent those variations in production are likely to indirectly impact the economy due to welfare losses, and welfare effects of price increase due to the reduced supply (Narita et al., 2012), changes in job opportunities, and general reverberation into the wider economy. As Richards et al. (2015b) stated “OA (*sic*) itself cannot be mitigated through fisheries management, however management can be used to reduce the negative effects and take advantage of positive effects associated with this phenomenon”.

4. Conclusion

OA is likely to have negative effects throughout the life cycle of oysters, although the effects may be difficult to decipher due to other stressors acting on multiple life-history stages (Byrne and Przeslawski, 2013; Knights and Walters, 2010). Acclimation, parental (hereditary) traits, or adaptation may well reduce the risk of negative consequences from OA, although the extent to which individuals can respond to the threat remains to be seen.

Oysters are a key ecological species that provide a plethora of ES to humans, but the provision, quantity, and quality of ESs in the future under climate change and OA remains uncertain. OA is occurring alongside other environmental and anthropogenic stressors, such as warming, hypoxia, variations in salinity, eutrophication, or metal contamination, that are likely to affect the organisms’ responses. The outcomes of multi-stressor interactions are difficult to predict and seem highly context-specific (see the reviews on the impacts of ocean warming and acidification by Byrne, 2011; Byrne and Przeslawski, 2013; and Harvey et al., 2013). Future studies should consider the combination of multiple stressors, but should also focus on adult oysters in the aim to link individual and population responses with the provision of associated ESs. The consequences of OA on oysters are already being felt in parts of the world (Cooley et al., 2015), where natural populations and hatcheries have been negatively impacted upon; therefore ocean acidification will likely put increased pressure on food security in the future, by reducing harvest and aquaculture productions. Predicted levels of OA are likely to hold a number of other significant social and economic consequences that goes beyond oyster production from harvest and aquaculture, such as impoverished water quality, reduced shoreline protection, or altered well-being.

The few studies to date that estimate the value of oyster-derived ESs give an insight into the importance and value of oysters to the environment and society. Whilst there is some variation in the economic value of oyster-derived ESs due to local and/or regional differences in societal value placed on those services, the role of oysters in supporting a healthy and functioning ecosystem is clear, but which is under threat from OA. Further assessments of the social and economic impacts of OA on oysters and oyster reefs are needed to emphasise the ‘value’ of oysters to society, such that necessary steps are taken to ensure their long-term future.

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Table 1 (web version (colour); print (grayscale)): Ecosystem goods and services provided by oysters and oyster reefs, following the ODEMM Linkage Framework description (White et al., 2013), and the potential impacts of ocean acidification (OA). '√' indicates that the service is provided by oysters, 'χ' indicates the service is not provided (according to the available literature). Direction of arrows indicates expected change in the ecosystem service (i.e. ↑ indicates increase in ES provision, ↓ a decrease in ES provision). '~' indicates that no consensus is reached or the change is context-specific.

	Marine Ecosystem Goods and Services	**Provided by Oysters or Oyster Reefs?**	**Estimated Value?**	**Affected by OA?**
Habitat	Lifecycle maintenance	√ *(assumed from 3-D structure)*	*Unknown*	*Yes* ↓~
	Gene pool protection	√ *(assumed from 3-D structure)*	*Unknown*	*Yes* ↓~
Provisioning	Sea Food	√ *(harvest, aquaculture, extended fisheries)*	\$20 850-\$52 224/hectare of reef *(oyster harvest value- Grabowski et al. (2012))* \$4123/year/hectare *(extended fisheries- Grabowski et al. (2012))* 809.7\$/tonne *(aquaculture production (FAO data*†*))*	*Yes* ↓ or ↑ ~
	Sea Water	X	X	X
	Raw materials	√ *(clutch material, construction material)*	\$7-10 lb^{-1} *(Baywater Oyster Seeds LLC)* \$17 yd^{-3} *(Pontchartrain Materials Corp., New Orleans)* \$17 yd^{-3} *(LDWF, 2004)* ~\$126/ton *(Kwon et al., 2004)*	*Yes* ↓~
	Genetic resources	√ *(aquaculture bred lines/triploid)*	*Unknown*	*Unknown*

	Medicinal resources	X	X	X
	Ornamental resources	√ *(shell collection)*	*~\$13m*$^{-3}$ (Lemasson, unpublished)	*Yes ↓~*
Regulating	Air purification	X	X	X
	Climate regulation (incl. carbon sequestration)	√ *(carbon sequestration)*	*Unknown*	*Yes ↓~*
	Disturbance prevention or moderation	√	Upward of $6 million *(for coastal defence structures- Firth et al., 2014)*	*Yes ↓~*
	Regulation of water flows	X	X	X
	Waste treatment (esp. water purification)	√ *(water purification, Chl-a removal, nutrient cycling)*	$1385-$6716/yr/ha. (Grabowski et al., 2012) $314 836/yr *(Newell et al., 2005)* $18 135/million oysters *(Kasperski and Wieland, 2009)* $3000/ac./yr *(Piehler and Smyth, 2011)* $293 993/yr *(Beseres-Pollack et al., 2013)*	*Yes ↓~*
	Coastal erosion prevention	√ *(shoreline stabilization, erosion prevention)*	*Upward of $6 million for coastal defence structures (Firth et al. 2014)*	*Yes ↓~*
	Biological control	√ *(facilitate submerged aquatic vegetation)*	*Unknown*	*Yes ↓~*
Cultural	Aesthetic information	X	X	X
	Recreation & leisure	√	$222 million *(U.S. National Research Council, 2004)*	*Yes ↓~*
	Inspiration for culture, art and design	X	X	X
	Spiritual experience	√ *(assumed)*	*Unknown*	*Unknown*

	Information for cognitive development	√ *(assumed)*	*Unknown*	*Unknown*
	Cultural Heritage and Identity	√ *(sense of tradition, oyster festivals)*	*Unknown*	*Unknown*

Figure 1: Categories of ecosystem goods and services, as described (left) in the Millennium Ecosystem Assessment (MEA, 2005), and additional examples (right) from the ODEMM Linkage Framework (White et al., 2013).

Figure 2: Total Economic Value framework (modified from Herbert et al., 2012).

Figure 3: Relationships between ocean acidification effects, various levels of biological complexity, the provision of ecosystem services, and the associated social and economic effects (adapted from Le Quesne and Pinnegar, 2012).

Figure 4: Conceptual diagram depicting some of the ecosystem services provided by oyster reefs (right) and the potential effects of ocean acidification on their provision (left). SAV=Submerged Aquatic Vegetation (Figure created by the authors, symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)).

Figure 1

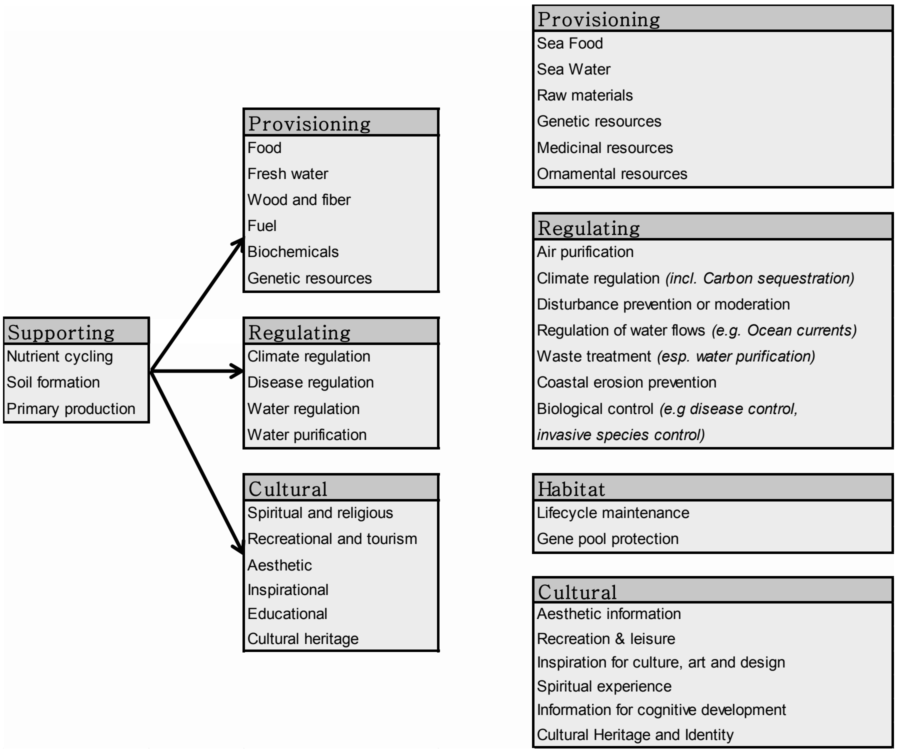

Supporting
Nutrient cycling
Soil formation
Primary production
Provisioning
Food
Fresh water
Wood and fiber
Fuel
Biochemicals
Genetic resources
Regulating
Climate regulation
Disease regulation
Water regulation
Water purification
Cultural
Spiritual and religious
Recreational and tourism
Aesthetic
Inspirational
Educational
Cultural heritage
Provisioning
Sea Food
Sea Water
Raw materials
Genetic resources
Medicinal resources
Ornamental resources
Regulating
Air purification
Climate regulation *(incl. Carbon sequestration)*
Disturbance prevention or moderation
Regulation of water flows *(e.g. Ocean currents)*
Waste treatment *(esp. water purification)*
Coastal erosion prevention
Biological control *(e.g disease control, invasive species control)*
Habitat
Lifecycle maintenance
Gene pool protection
Cultural
Aesthetic information
Recreation & leisure
Inspiration for culture, art and design
Spiritual experience
Information for cognitive development
Cultural Heritage and Identity

Figure 2: (web version)

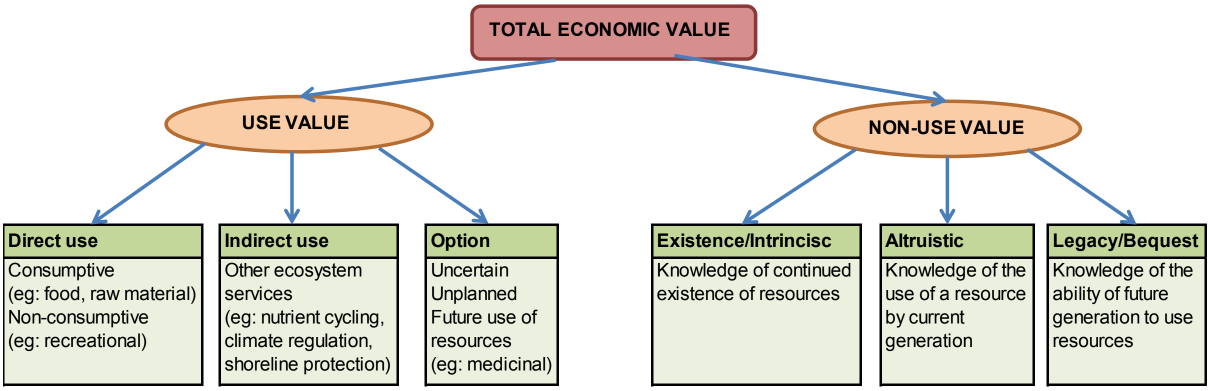


Figure 2: (print version)

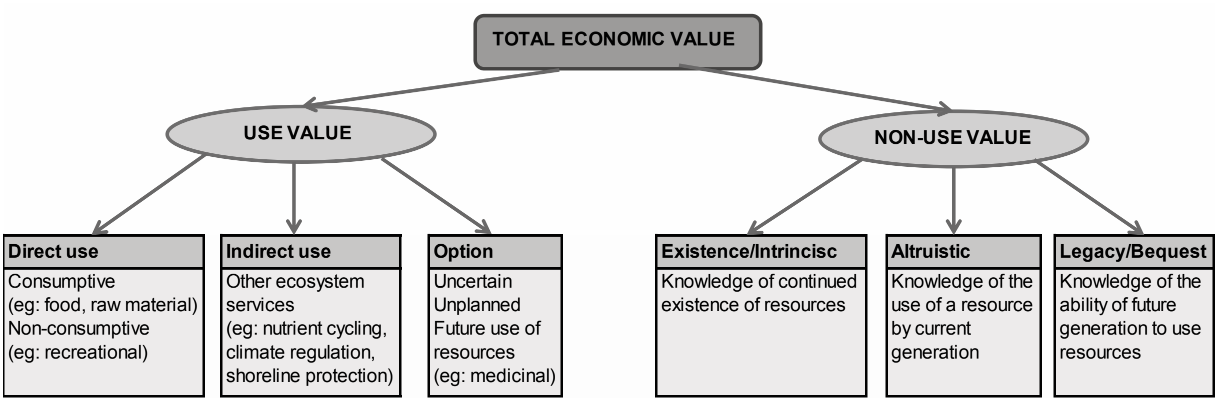


Figure 3: (web version)

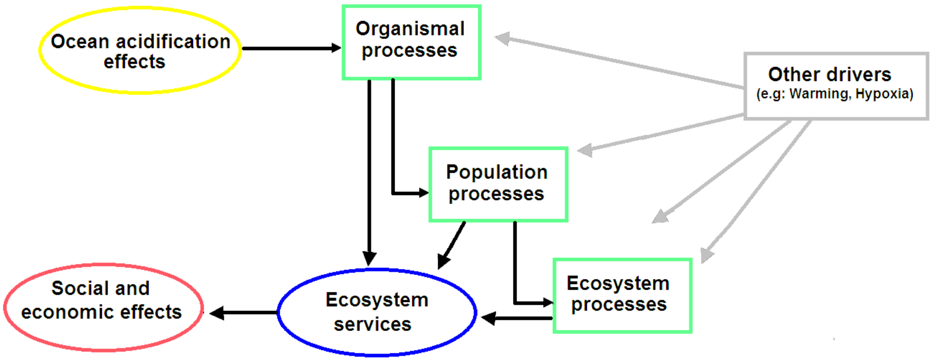


Figure 3: (print version)

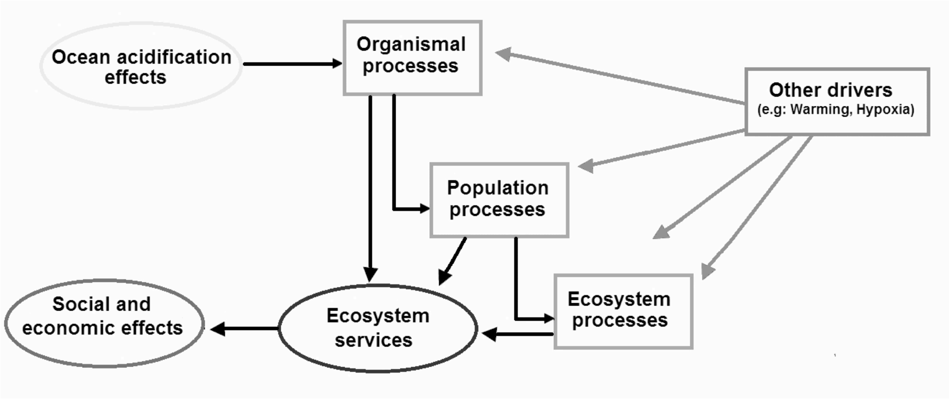
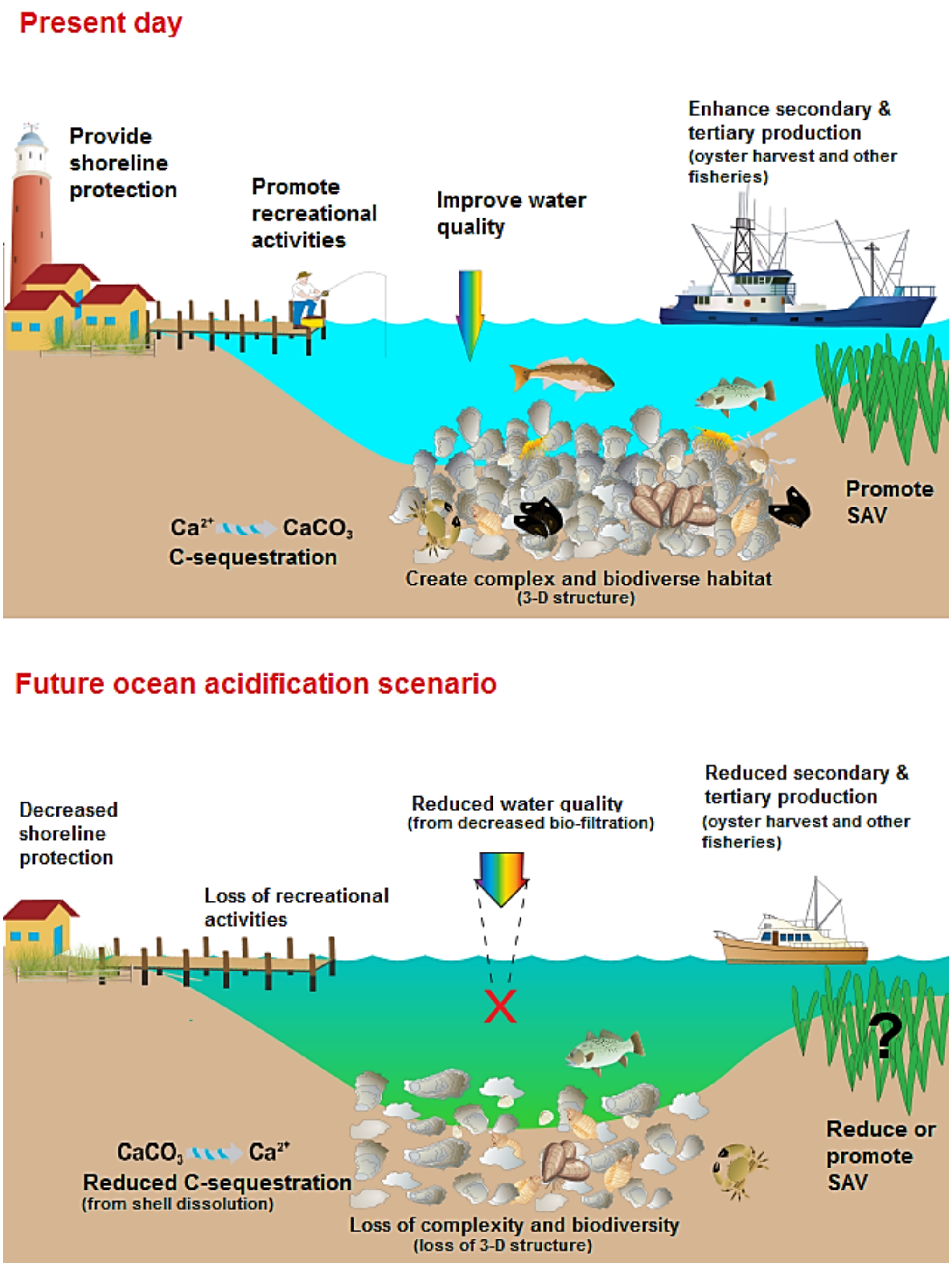


Figure 4: (web and print versions)



Highlights:

- Ocean acidification (OA) threatens all stages of the life-cycle of oysters.
- Oyster reefs provide numerous ecosystem services (ES)
- The delivery of ESs associated with healthy oyster reefs may be threatened by OA.
- Further studies linking OA and ES are urgently needed.