2017-02-21

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

Lemasson, Anaëlle

<http://hdl.handle.net/10026.1/8027>

10.1016/j.jembe.2017.01.019

Journal of Experimental Marine Biology and Ecology

Elsevier BV

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

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

Anaëlle J. Lemasson^a, Stephen Fletcher^{b,c}, Jason M Hall-Spencer^a, Antony M. Knights^a

^a Marine Biology and Ecology Research Centre, School of Marine Science and Engineering, Plymouth University, Davy Building, Plymouth, PL4 8AA, UK

^b UNEP World Conservation Monitoring Centre (UNEP-WCMC), Cambridge, CB3 0DL, UK

^c Centre for Marine and Coastal Policy Research (MarCoPol), School of Marine Science and Engineering, Plymouth University, Plymouth, PL4 8AA, UK

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 CO₂, altering oceanic carbonate chemistry by reducing carbonate ion concentrations (CO₃²⁻), 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 CO₂ 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

101

102 The planktic larval stage is a crucial life-history stage for many benthic
103 organisms and changes in development, performance or survival of this stage
104 can critically influence juvenile-adult population dynamics and ecosystem
105 functioning (Bachelet, 1990; Green et al., 2004; Rumrill, 1990). The early
106 development stages of marine calcifiers were quickly identified as particularly
107 vulnerable to OA, with the potential to alter population size and dynamics, and
108 community structure (Kurihara, 2008). As such, there has been a burgeoning
109 literature describing larval responses to OA (reviewed in Albright, 2011; Byrne,
110 2011; Przeslawski et al., 2014; Ross et al., 2011).

111

112 OA has been shown to induce narcotic effects on motile life-history stages,
113 reducing fertilisation success (Byrne, 2011). In a number of instances, OA
114 effects include reduced sperm motility, reductions in fertilisation success and
115 hatching rates of embryos (Barros et al., 2013; Parker et al., 2009; Parker et al.,
116 2010), although in the case of Parker et al. (2009), changes could not be solely
117 attributed to OA due to the effects being conflated with suboptimal culture
118 temperatures. However, OA-induced narcosis has not been consistently shown,
119 with disparity between studies of the same species (e.g. Kurihara et al., 2007;
120 Parker et al., 2012). Parker et al. (2012) suggest this disparity may be the result
121 of intraspecific phenotypic plasticity, whereas Byrne (2011) argues that the
122 fertilisation process in marine invertebrates can be resilient to fluctuations in pH
123 and may not be a reliable end-point. Neither Parker et al. (2012) or Byrne's
124 (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 $p\text{CO}_2$, 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

323

324 There are concerns over whether species will be able to adapt to the current
325 unprecedented rates of environmental change (Somero, 2010; Sunday et al.,
326 2014; Visser, 2008). Fast-generating species such as the pond algae,
327 *Chlamydomonas*, did not show evidence of adaptation to acidified conditions
328 after 1000 generations (Collins and Bell, 2004), although recently, the marine
329 polychaete, *Ophryotrocha labronica*, demonstrated acclimation after just two
330 generations (Rodríguez-Romero et al., 2015) indicating vastly different
331 propensity for adaptation. It might be reasonable to assume that long-lived,
332 slow generation time species, such as oysters, are even less likely to evolve
333 rapidly (Barry et al., 2011; Byrne, 2011). However, Parker et al. (2015; 2012)
334 demonstrated conferred tolerance from adults exposed to elevated CO₂ to their
335 offspring (also dependent on if the oysters originated from wild or aquaculture-
336 reared populations), suggesting hereditary traits as a mechanism of resilience.
337 But as in fast generation time species, the potential for adaptation may be
338 species-specific, as well as dependent on the heritage of the individual (Parker
339 et al., 2010; Parker et al., 2011 respectively; Thompson et al., 2015).

340

341 A possible mechanism through which resilience to environmental stress can be
342 achieved may be linked to the 'quality' of the environment. In the Baltic Sea,
343 seasonal upwelling of eutrophic water leads to very high CO₂ levels and
344 phytoplankton blooms, nevertheless, blue mussel reefs are able maintain their
345 structure and function. Thomsen et al. (2012) argued that the high food supply
346 allows the mussels to offset the metabolic costs of hypercapnia (Thomsen et al.,
347 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 CO₂ 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 CO₂ (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 healthy 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 data¹).

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

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.

5. Acknowledgements

This research is supported by a grant awarded to AMK, JHS, and SF by the School of Marine Science and Engineering, Plymouth University, as part of the PhD research of AJL. Thank you also to Bayden Russell (editor) and two anonymous reviewers whose comments greatly helped to improve this manuscript.

6. References

- Albright, R., 2011. Reviewing the effects of ocean acidification on sexual reproduction and early life history stages of reef-building corals. *Journal of Marine Biology*, 1-14.
- Alleway, H.K., Connell, S.D., 2015. Loss of an ecological baseline through the eradication of oyster reefs from coastal ecosystems and human memory. *Conservation Biology*.

819 Anil, A.C., Desai, D., Khandeparker, L., 2001. Larval development and metamorphosis in *Balanus*
820 *amphitrite* Darwin (Cirripedia; Thoracica): significance of food concentration, temperature and
821 nucleic acids. *Journal of Experimental Marine Biology and Ecology* 263, 125-141.

822 Asplund, M.E., Baden, S.P., Russ, S., Ellis, R.P., Gong, N., Hernroth, B.E., 2014. Ocean acidification
823 and host-pathogen interactions: blue mussels, *Mytilus edulis*, encountering *Vibrio tubiashii*.
824 *Environmental microbiology* 16, 1029-1039.

825 Bachelet, G., 1990. Recruitment of soft-sediment infaunal invertebrates: the importance of
826 juvenile benthic stages. *La Mer* 28, 199-210.

827 Bailey, C., 2008. Human dimension of an ecosystem approach to aquaculture, in: Soto D, A.-M.J.,
828 Hishamunda N (Ed.), *Building an ecosystem approach to aquaculture*. FAO Fisheries and
829 Aquaculture Proceedings. No. 14. Rome, Italy: Food and Agriculture Organization,
830 FAO/Universitat de les Illes Balears Expert Workshop, 7–11 May 2007, Palma de Mallorca,
831 Spain, pp. 37–42.

832 Bamber, R.N., 1990. The effects of acidic seawater on three species of lamellibranch mollusc.
833 *Journal of Experimental Marine Biology and Ecology* 143, 181-191.

834 Barros, P., Sobral, P., Range, P., Chícharo, L., Matias, D., 2013. Effects of sea-water acidification
835 on fertilization and larval development of the oyster *Crassostrea gigas*. *Journal of*
836 *Experimental Marine Biology and Ecology* 440, 200-206.

837 Barry, J.P., Widdicombe, S., Hall-Spencer, J.M., 2011. Effects of ocean acidification on marine
838 biodiversity and ecosystem function. *Ocean Acidification*, 192-209.

839 Barton, A., Waldbusser, G., Feely, R., Weisberg, S., Newton, J., Hales, B., Cudd, S., Eudeline, B.,
840 Langdon, C., Jefferds, I., King, T., Suhrbier, A., McLaughlin, K., 2015. Impacts of coastal
841 acidification on the Pacific Northwest shellfish industry and adaptation strategies implemented
842 in response. *Oceanography* 25, 146-159.

843 Basso, L., Hendriks, I.E., Rodríguez-Navarro, A.B., Gambi, M.C., Duarte, C.M., 2015. Extreme pH
844 conditions at a natural CO₂ vent system (Italy) affect growth, and survival of juvenile Pen shells
845 (*Pinna nobilis*). Estuaries and Coasts.

846 Beaumont, N.J., Austen, M.C., Atkins, J.P., Burdon, D., Degraer, S., Dentinho, T.P., Deros, S.,
847 Holm, P., Horton, T., van Ierland, E., Marboe, A.H., Starkey, D.J., Townsend, M., Zarzycki, T.,
848 2007. Identification, definition and quantification of goods and services provided by marine
849 biodiversity: implications for the ecosystem approach. Mar Pollut Bull 54, 253-265.

850 Beck, M.W., Brumbaugh, R.D., Airoidi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar,
851 G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G., Guo,
852 X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and
853 management. BioScience 61, 107-116.

854 Beesley, A., Lowe, D.M., Pascoe, C.K., Widdicombe, S., 2008. Effects of CO₂-induced seawater
855 acidification on the health of *Mytilus edulis*. Climate Res 37, 215-225.

856 Beniash, E., Ivanina, A., Lieb, N.S., Kurochkin, I., Sokolova, I.M., 2010. Elevated level of carbon
857 dioxide affects metabolism and shell formation in oysters *Crassostrea virginica* (Gmelin).
858 Marine Ecology Progress Series 419, 95-108.

859 Beseres-Pollack, J., Yoskowitz, D., Kim, H.-C., Montagna, P.A., 2013. Role and value of nitrogen
860 regulation provided by oysters (*Crassostrea virginica*) in the Mission-Aransas Estuary, Texas,
861 USA. PloS one 8, e65314.

862 Bibby, R., Widdicombe, S., Parry, H., Spicer, J., Pipe, R., 2008. Effects of ocean acidification on
863 the immune response of the blue mussel *Mytilus edulis*. Aquatic Biology 2, 67-74.

864 Bosello, F., Delpiazzi, E., Eboli, F., 2015. Acidification in the Mediterranean sea: impacts and
865 adaptation strategies. Review of Environment, Energy and Economics (Re3), Forthcoming.

866 Brander, L.M., Rehdanz, K., Tol, R.S., Van Beukering, P.J., 2012. The economic impact of ocean
867 acidification on coral reefs. Climate Change Economics 3.

868 Brečević, L., Nielsen, A.E., 1989. Solubility of amorphous calcium carbonate. *J Cryst Growth* 98,
869 504-510.

870 Brodie, J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M.,
871 Steinke, M., Yesson, C., Anderson, K.M., Asnaghi, V., Brownlee, C., Burdett, H.L., Burrows, M.T.,
872 Collins, S., Donohue, P.J., Harvey, B., Foggo, A., Noisette, F., Nunes, J., Ragazzola, F., Raven, J.A.,
873 Schmidt, D.N., Suggett, D., Teichberg, M., Hall-Spencer, J.M., 2014. The future of the northeast
874 Atlantic benthic flora in a high CO₂ world. *Ecology and Evolution* 4, 2787-2798.

875 Brumbaugh, R.D., Beck, M.W., Hancock, B., Meadows, A.W., Spalding, M., zu Ermgassen, P.,
876 2010. Changing a management paradigm and rescuing a globally imperiled habitat. *National*
877 *Wetlands Newsletter*, 16-20.

878 Byrne, M., 2011. Impact of ocean warming and ocean acidification on marine invertebrate life
879 history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanography*
880 *and Marine Biology: An Annual Review* 49, 1-42.

881 Byrne, M., Przeslawski, R., 2013. Multistressor impacts of warming and acidification of the ocean
882 on marine invertebrates' life histories. *Integrative and comparative biology* 53, 582-596.

883 Callaway, R., Shinn, A.P., Grenfell, S.E., Bron, J.E., Burnell, G., Cook, E.J., Crumlish, M., Culloty, S.,
884 Davidson, K., Ellis, R.P., Flynn, K.J., Fox, C., Green, D.M., Hays, G.C., Hughes, A.D., Johnston, E.,
885 Lowe, C.D., Lupatsch, I., Malham, S., Mendzil, A.F., Nickell, T., Pickerell, T., Rowley, A.F., Stanley,
886 M.S., Tocher, D.R., Turnbull, J.F., Webb, G., Wootton, E., Shields, R.J., 2012. Review of climate
887 change impacts on marine aquaculture in the UK and Ireland. *Aquatic Conservation: Marine*
888 *and Freshwater Ecosystems* 22, 389-421.

889 Çath, A., Bozkurt, M., Küçükyılmaz, K., Çinar, M., Bintaş, E., Çöven, F., Atik, H., 2012.
890 Performance and egg quality of aged laying hens fed diets supplemented with meat and bone
891 meal or oyster shell meal. *South African Journal of Animal Science* 42, 74-82.

892 Cerco, C.F., Noel, M.R., 2007. Can oyster restoration reverse cultural eutrophication in
893 Chesapeake Bay? *Estuaries and Coasts* 30, 331-343.

894 Christen, N., Calosi, P., McNeill, C.L., Widdicombe, S., 2013. Structural and functional
895 vulnerability to elevated $p\text{CO}_2$ in marine benthic communities. *Marine Biology* 160, 2113-2128.

896 Cigliano, M., Gambi, M.C., Rodolfo-Metalpa, R., Patti, F.P., Hall-Spencer, J.M., 2010. Effects of
897 ocean acidification on invertebrate settlement at volcanic CO_2 vents. *Marine Biology* 157,
898 2489-2502.

899 Ciuriak, N., 2012. The quiet tsunamis: the ecological, economic, social, and political consequences
900 of ocean acidification. *Paterson Review of International Affairs* 12, 123-143.

901 Clarkson, M., Kasemann, S., Wood, R., Lenton, T., Daines, S., Richoz, S., Ohnemuehler, F., Meixner,
902 A., Poulton, S., Tipper, E., 2015. Ocean acidification and the Permo-Triassic mass extinction.
903 *Science* 348, 229-232.

904 Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M.W., Posey, M.H., Powers,
905 S.P., Tolley, S., 2007. Ecosystem services related to oyster restoration. *Marine Ecology Progress*
906 *Series* 341, 303-307.

907 Coen, L.D., Luckenbach, M.W., Breitburg, D.L., 1999. The role of oyster reefs as essential fish
908 habitat: a review of current knowledge and some new perspectives, *American Fisheries Society*
909 *Symposium*, pp. 438-454.

910 Collins, S., Bell, G., 2004. Phenotypic consequences of 1,000 generations of selection at elevated
911 CO_2 in a green alga. *Nature* 431, 566-569.

912 Comeau, S., Carpenter, R.C., Lantz, C.A., Edmunds, P.J., 2015. Ocean acidification accelerates
913 dissolution of experimental coral reef communities. *Biogeosciences* 12, 365-372.

914 Cooley, S.R., 2012. How human communities could 'feel' changing ocean biogeochemistry.
915 *Current Opinion in Environmental Sustainability* 4, 258-263.

916 Cooley, S.R., Doney, S.C., 2009. Anticipating ocean acidification's economic consequences for
917 commercial fisheries. *Environmental Research Letters* 4, 024007.

918 Cooley, S.R., Kite-Powell, H.L., Doney, S.C., 2009. Ocean acidification's potential to alter global
919 marine ecosystem services. *Oceanography* 22.

920 Cooley, S.R., Lucey, N., Kite-Powell, H., Doney, S.C., 2012. Nutrition and income from molluscs
 921 today imply vulnerability to ocean acidification tomorrow. *Fish and Fisheries* 13, 182-215.

922 Cooley, S.R., Ono, C.R., Melcer, S., Roberson, J., 2015. Community-level actions that can address
 923 ocean acidification. *Frontiers in Marine Science* 2.

924 De Groot, R.S., Wilson, M.A., Boumans, R.M., 2002. A typology for the classification, description
 925 and valuation of ecosystem functions, goods and services. *Ecological Economics* 41, 393-408.

926 DEFRA, 2013. An introductory guide to valuing ecosystem services. Department for Environment,
 927 Food and Rural Affairs.

928 Dehon, D.D., 2010. Investigating the use of bioengineered oyster reefs as a method of shoreline
 929 protection and carbon storage. MSc Thesis. Louisiana State University.

930 Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar, S., Bergstrom, P.W.,
 931 Batiuk, R.A., 1993. Assessing water quality with submersed aquatic vegetation. *BioScience*, 86-
 932 94.

933 Díaz, S., Fargione, J., Chapin, F.S., III, Tilman, D., 2006. Biodiversity loss threatens human well-
 934 being. *PLoS Biol* 4, e277.

935 Dickinson, G.H., Ivanina, A.V., Matoo, O.B., Portner, H.O., Lannig, G., Bock, C., Beniash, E.,
 936 Sokolova, I.M., 2012. Interactive effects of salinity and elevated CO₂ levels on juvenile eastern
 937 oysters, *Crassostrea virginica*. *The Journal of experimental biology* 215, 29-43.

938 Dorfmeier, E.M., 2012. Ocean acidification and disease: How will a changing climate impact
 939 *Vibrio tubiashii* growth and pathogenicity to Pacific oyster larvae?, School of Aquatic and
 940 Fishery Sciences. University of Washington.

941 Dove, M.C., Sammut, J., 2007. Impacts of estuarine acidification on survival and growth of
 942 Sydney rock oysters *Saccostrea glomerata* (Gould 1850). *Journal of Shellfish Research* 26, 519-
 943 527.

944 Dupont, S., Hall, E., Calosi, P., Lundve, B., 2014. First evidence of altered sensory quality in a
 945 shellfish exposed to decreased pH relevant to ocean acidification. *Journal of Shellfish Research*
 946 33, 857-861.

947 Dupont, S., Thorndyke, M., 2012. Relationship between CO₂-driven changes in extracellular
 948 acid–base balance and cellular immune response in two polar echinoderm species. *Journal of*
 949 *Experimental Marine Biology and Ecology* 424–425, 32-37.

950 Dyer, C.L., Leard, R.L., 1994. Folk management in the oyster fishery of the US Gulf of Mexico.
 951 *Folk Management in the World's Fisheries*, 55-89.

952 Ekstrom, J.A., Suatoni, L., Cooley, S.R., Pendleton, L.H., Waldbusser, G.G., Cinner, J.E., Ritter, J.,
 953 Langdon, C., van Hooidonk, R., Gledhill, D., Wellman, K., Beck, M.W., Brander, L.M., Rittschof,
 954 D., Doherty, C., Edwards, P.E.T., Portela, R., 2015. Vulnerability and adaptation of US
 955 shellfisheries to ocean acidification. *Nature Clim. Change* 5, 207-214.

956 Ellis, R.P., 2013. PhD Thesis: The impact of ocean acidification, increased seawater temperature
 957 and a bacterial challenge on the immune response and physiology of the blue mussel, *Mytilus*
 958 *edulis*. Plymouth University.

959 Elston, R.A., Hasegawa, H., Humphrey, K.L., Polyak, I.K., Hase, C.C., 2008. Re-emergence of *Vibrio*
 960 *tubiaschii* in bivalve shellfish aquaculture: severity, environmental drivers, geographic extent
 961 and management. *Dis Aquat Organ* 82, 119-134.

962 Fabricius, K.E., De'ath, G., Noonan, S., Uthicke, S., 2014. Ecological effects of ocean acidification
 963 and habitat complexity on reef-associated macroinvertebrate communities. *P Roy Soc B-Biol*
 964 *Sci* 281, 20132479.

965 FAO, 2014 The State of World Fisheries and Aquaculture 2014. Rome. 223 pp.

966 Feely, R.A., Sabine, C.L., Hernandez-Ayon, J.M., Ianson, D., Hales, B., 2008. Evidence for
 967 upwelling of corrosive" acidified" water onto the continental shelf. *Science* 320, 1490-1492.

968 Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoidi, L., Bouma, T.J., Bozzeda, F., Ceccherelli,
 969 V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson,

970 J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., van Belzen, J., Hawkins,
 971 S.J., 2014. Between a rock and a hard place: Environmental and engineering considerations
 972 when designing coastal defence structures. *Coastal Engineering* 87, 122-135.

973 Fletcher, S., Rees, S., Gall, S., Shellock, R., Dodds, W., Rodwell, L., 2014. Assessing the socio-
 974 economic benefits of marine protected areas. A report for Natural Resources Wales by the
 975 Centre for Marine and Coastal Policy Research, Plymouth University.

976 Fletcher, S., Saunders, J., Herbert, R., Roberts, C., Dawson, K., 2012. Description of the
 977 ecosystem services provided by broad-scale habitats and features of conservation importance
 978 that are likely to be protected by Marine Protected Areas in the Marine Conservation Zone
 979 Project area., Natural England Commissioned Reports 088.

980 Friedrich, L.A., Dodds, W., Philippe, M., Glegg, G., Fletcher, S., Bailly, D., 2015. Improving
 981 stakeholder engagement in marine management through ecosystem service assessment. A
 982 guide for practitioners based on experience from the VALMER project.

983 Frommel, A.Y., Maneja, R., Lowe, D., Malzahn, A.M., Geffen, A.J., Folkvord, A., Piatkowski, U.,
 984 Reusch, T.B.H., Clemmesen, C., 2012. Severe tissue damage in Atlantic cod larvae under
 985 increasing ocean acidification. *Nature Climate Change* 2, 42-46.

986 Fulton, E.A., 2011. Interesting times: winners, losers, and system shifts under climate change
 987 around Australia. *ICES Journal of Marine Science* 68, 1329-1342.

988 Gattuso, J.P., Hoegh-Guldberg, O., Pörtner, H.O., 2014. Cross-chapter box on ocean acidification,
 989 in: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee,
 990 M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S.,
 991 Mastrandrea, P.R., White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and*
 992 *Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth*
 993 *Assessment Report of the Intergovernmental Panel of Climate Change.* Cambridge University
 994 Press, Cambridge, United Kingdom and New York, NY, USA, pp. 97-100.

995 Gattuso, J.P., Magnan, A., Bille, R., Cheung, W.W., Howes, E.L., Joos, F., Allemand, D., Bopp, L.,
 996 Cooley, S.R., Eakin, C.M., Hoegh-Guldberg, O., Kelly, R.P., Portner, H.O., Rogers, A.D., Baxter,
 997 J.M., Laffoley, D., Osborn, D., Rankovic, A., Rochette, J., Sumaila, U.R., Treyer, S., Turley, C.,
 998 2015. Contrasting futures for ocean and society from different anthropogenic CO₂ emissions
 999 scenarios. *Science* 349, aac4722.

1000 Gaylord, B., Hill, T.M., Sanford, E., Lenz, E.A., Jacobs, L.A., Sato, K.N., Russell, A.D., Hettinger, A.,
 1001 2011. Functional impacts of ocean acidification in an ecologically critical foundation species.
 1002 *The Journal of Experimental Biology* 214, 2586-2594.

1003 Gazeau, F., Alliouane, S., Correa, M.L., Gentile, M., Bock, C., Hirse, T., Bramanti, L., Pörtner, H.-O.,
 1004 Ziveri, P., 2014. Impact of ocean acidification and warming on the Mediterranean mussel
 1005 (*Mytilus galloprovincialis*). *Frontiers in Marine Science* 1.

1006 Gazeau, F., Gattuso, J.P., Dawber, C., Pronker, A.E., Peene, F., Peene, J., Heip, C.H.R., Middelburg,
 1007 J.J., 2010. Effect of ocean acidification on the early life stages of the blue mussel *Mytilus edulis*.
 1008 *Biogeosciences* 7, 2051-2060.

1009 Gazeau, F., Gattuso, J.P., Greaves, M., Elderfield, H., Peene, J., Heip, C.H., Middelburg, J.J., 2011.
 1010 Effect of carbonate chemistry alteration on the early embryonic development of the Pacific
 1011 oyster (*Crassostrea gigas*). *PloS one* 6, e23010.

1012 Gazeau, F., Parker, L.M., Comeau, S., Gattuso, J.-P., O'Connor, W.A., Martin, S., Pörtner, H.-O.,
 1013 Ross, P.M., 2013. Impacts of ocean acidification on marine shelled molluscs. *Marine Biology*
 1014 160, 2207-2245.

1015 Gazeau, F., Quiblier, C., Jansen, J.M., Gattuso, J.-P., Middelburg, J.J., Heip, C.H.R., 2007. Impact
 1016 of elevated CO₂ on shellfish calcification. *Geophysical Research Letters* 34.

1017 Geraldi, N.R., Powers, S.P., Heck, K.L., Cebrian, J., 2009. Can habitat restoration be redundant?
 1018 Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks.
 1019 *Marine Ecology Progress Series* 389, 171-180.

1020 Gobler, C.J., Talmage, S.C., 2014. Physiological response and resilience of early life-stage Eastern
1021 oysters (*Crassostrea virginica*) to past, present and future ocean acidification. Conservation
1022 Physiology 2.

1023 Gosselin, L.A., Qian, P.-Y., 1997. Juvenile mortality in benthic marine invertebrates. Marine
1024 Ecology Progress Series 146, 265-282.

1025 Grabowski, J.H., Brumbaugh, R.D., Conrad, R.F., Keeler, A.G., Opaluch, J.J., Peterson, C.H., Piehler,
1026 M.F., Powers, S.P., Smyth, A.R., 2012. Economic valuation of ecosystem services provided by
1027 oyster reefs. BioScience 62, 900-909.

1028 Grabowski, J.H., Peterson, C.H., 2007. Restoring oyster reefs to recover ecosystem services, in:
1029 Kim Cuddington, J.E.B.W.G.W., Alan, H. (Eds.), Theoretical Ecology Series. Academic Press, pp.
1030 281-298.

1031 Green, M.A., Jones, M.E., Boudreau, C.L., Moore, R.L., Westman, B.A., 2004. Dissolution
1032 mortality of juvenile bivalves in coastal marine deposits. Limnology and Oceanography 49, 727-
1033 734.

1034 Grizzle, R.E., Greene, J.K., Coen, L.D., 2008. Seston removal by natural and constructed intertidal
1035 Eastern oyster (*Crassostrea virginica*) reefs: a comparison with previous laboratory studies,
1036 and the value of in situ methods. Estuaries and Coasts 31, 1208-1220.

1037 Guo, X., Huang, M., Pu, F., You, W., Ke, C., 2015. Effects of ocean acidification caused by rising
1038 CO₂ on the early development of three mollusks. Aquatic Biology 23, 147-157.

1039 Haigh, R., Ianson, D., Holt, C.A., Neate, H.E., Edwards, A.M., 2015. Effects of ocean acidification
1040 on temperate coastal marine ecosystems and fisheries in the northeast pacific. PloS one 10,
1041 e0117533.

1042 Hall-Spencer, J., Allen, R., 2015. The impact of CO₂ emissions on 'nuisance' marine species.
1043 Research and Reports in Biodiversity Studies, 33.

1044 Hall, S.G., Risinger, J.D., Farlow, J., 2011. Ecological engineering of artificial oyster reefs to
1045 enhance carbon sequestration via the algae-oyster complex. Conference proceedings.
1046 American Society of Agricultural and Biological Engineers, p. 1.

1047 Harvey, B.P., Gwynn-Jones, D., Moore, P.J., 2013. Meta-analysis reveals complex marine
1048 biological responses to the interactive effects of ocean acidification and warming. Ecology and
1049 Evolution 3, 1016-1030.

1050 Henderson, J., O'Neil, J., 2003. Economic values associate with construction of oyster reefs.
1051 Corps of Engineers, EMRRP Technical Notes Collection (ERDC TN-EMRRP-ER-01), US Army
1052 Engineer Research and Development Center, Vicksburg, MS.

1053 Heral, M., 1989. Traditional oyster culture in France, Barnabe. Aquaculture, pp. 342-387.

1054 Herbert, R.J.H., Robert, C., Humphreys, J., Fletcher, S., 2012. The Pacific Oyster (*Crassostrea*
1055 *gigas*) in the UK: economic, legal and environmental issues associated with its cultivation, wild
1056 establishment and exploitation. Report for the Shellfish Association of Great Britain.

1057 Hettinger, A., Sanford, E., Hill, T., Hosfelt, J., Russell, A., Gaylord, B., 2013a. The influence of food
1058 supply on the response of Olympia oyster larvae to ocean acidification. Biogeosciences 10,
1059 6629-6638.

1060 Hettinger, A., Sanford, E., Hill, T.M., Lenz, E.A., Russell, A.D., Gaylord, B., 2013b. Larval carry-over
1061 effects from ocean acidification persist in the natural environment. Global Change Biology 19,
1062 3317-3326.

1063 Hettinger, A., Sanford, E., Hill, T.M., Russell, A.D., Sato, K.N.S., Hoey, J., Forsch, M., Page, H.N.,
1064 Gaylord, B., 2012. Persistent carry-over effects of planktonic exposure to ocean acidification in
1065 the Olympia oyster. Ecology 93, 2758-2768.

1066 Hickey, 2008. Carbon sequestration potential of shellfish. In Seminars in Sustainability.
1067 University of South Australia.

1068 Hilmi, N., Allemand, D., Cinar, M., Cooley, S., Hall-Spencer, J., Haraldsson, G., Hattam, C., Jeffree,
 1069 R., Orr, J., Rehdanz, K., Reynaud, S., Safa, A., Dupont, S., 2014. Exposure of Mediterranean
 1070 countries to ocean acidification. *Water* 6, 1719-1744.

1071 Hilmi, N., Allemand, D., Dupont, S., Safa, A., Haraldsson, G., Nunes, P.A., Moore, C., Hattam, C.,
 1072 Reynaud, S., Hall-Spencer, J.M., Fine, M., Turley, C., Jeffree, R., Orr, J., Munday, P.L., Cooley,
 1073 S.R., 2013. Towards improved socio-economic assessments of ocean acidification's impacts.
 1074 *Marine Biology* 160, 1773-1787.

1075 Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell,
 1076 C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R.,
 1077 Muthiga, N., Bradbury, R.H., Dubi, A., Hatzioios, M.E., 2007. Coral reefs under rapid climate
 1078 change and ocean acidification. *Science* 318, 1737-1742.

1079 Hoellein, T.J., Zarnoch, C.B., Grizzle, R.E., 2015. Eastern oyster (*Crassostrea virginica*) filtration,
 1080 biodeposition, and sediment nitrogen cycling at two oyster reefs with contrasting water
 1081 quality in Great Bay Estuary (New Hampshire, USA). *Biogeochemistry* 122, 113-129.

1082 Houlbrèque, F., Reynaud, S., Godinot, C., Oberhänsli, F., Rodolfo-Metalpa, R., Ferrier-Pagès, C.,
 1083 2015. Ocean acidification reduces feeding rates in the scleractinian coral *Stylophora pistillata*.
 1084 *Limnology and Oceanography* 60, 89-99.

1085 Hsu, T.C., 2009. Experimental assessment of adsorption of Cu^{2+} and Ni^{2+} from aqueous solution
 1086 by oyster shell powder. *Journal of Hazardous Materials* 171, 995-1000.

1087 Humphreys, J., Herbert, R.J.H., Roberts, C., Fletcher, S., 2014. A reappraisal of the history and
 1088 economics of the Pacific oyster in Britain. *Aquaculture* 428-429, 117-124.

1089 Ivanina, A.V., Hawkins, C., Sokolova, I.M., 2014. Immunomodulation by the interactive effects of
 1090 cadmium and hypercapnia in marine bivalves *Crassostrea virginica* and *Mercenaria mercenaria*.
 1091 *Fish and Shellfish Immunology* 37, 299-312.

1092 Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury,
1093 R.H., Cooke, R., Erlandson, J., Estes, J.A., 2001. Historical overfishing and the recent collapse of
1094 coastal ecosystems. *Science* 293, 629-637.

1095 Jones, C., Lawton, J., Shachak, M., 1996. *Organisms as Ecosystem Engineers*, Ecosystem
1096 Management. Springer New York, pp. 130-147.

1097 Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as
1098 physical ecosystem engineers. *Ecology* 78, 1946-1957.

1099 Kahn, J.R., Kemp, W.M., 1985. Economic losses associated with the degradation of an
1100 ecosystem: The case of submerged aquatic vegetation in Chesapeake Bay. *Journal of*
1101 *Environmental Economics and Management* 12, 246-263.

1102 Kasperski, S., Wieland, R., 2009. When is it optimal to delay harvesting? The role of ecological
1103 services in the Northern Chesapeake Bay oyster fishery. *Mar Resour Econ* 24, 361-385.

1104 Kellogg, M.L., Cornwell, J.C., Owens, M.S., Paynter, K.T., 2013. Denitrification and nutrient
1105 assimilation on a restored oyster reef. *Marine Ecology Progress Series* 480, 1-19.

1106 Kim, J.-H., Yu, O.H., Yang, E.J., Kang, S.-H., Kim, W., Choy, E.J., 2016. Effects of ocean acidification
1107 driven by elevated CO₂ on larval shell growth and abnormal rates of the venerid clam, *Macra*
1108 *veneriformis*. *Chin. J. Ocean. Limnol.*

1109 Kirby, M.X., 2004. Fishing down the coast: Historical expansion and collapse of oyster fisheries
1110 along continental margins. *Proceedings of the National Academy of Sciences of the United*
1111 *States of America* 101, 13096-13099.

1112 Knights, A.M., Culhane, F., Hussain, S.S., Papadopoulou, K.N., Piet, G.J., Raakær, J., Rogers, S.I.,
1113 Robinson, L.A., 2014. A step-wise process of decision-making under uncertainty when
1114 implementing environmental policy. *Environmental Science & Policy* 39, 56-64.

1115 Knights, A.M., Walters, K., 2010. Recruit-recruit interactions, density-dependent processes and
1116 population persistence in the eastern oyster *Crassostrea virginica*. *Marine Ecology Progress*
1117 *Series* 404, 79-90.

1118 Ko, W.K.G., Chan, V.B., Dineshram, R., Choi, K.S.D., Li, J.A., Ziniu, Y., Thiyagarajan, V., 2013. Larval
1119 and post-larval stages of Pacific oyster (*Crassostrea gigas*) are resistant to elevated CO₂. PloS
1120 One 8, e64147.

1121 Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., Fox, J., 2015. Community
1122 assembly, coexistence and the environmental filtering metaphor. Funct Ecol 29, 592-599.

1123 Kroeger, T., 2012. Dollars and Sense: Economic benefits and impacts from two oyster reef
1124 restoration projects in the Northern Gulf of Mexico., The Nature Conservancy.

1125 Kroeker, K.J., Kordas, R.L., Crim, R.N., Singh, G.G., 2010. Meta-analysis reveals negative yet
1126 variable effects of ocean acidification on marine organisms. Ecology Letters 13, 1419-1434.

1127 Kroeker, K.J., Micheli, F., Gambi, M.C., 2012. Ocean acidification causes ecosystem shifts via
1128 altered competitive interactions. Nature Climate Change 3, 156-159.

1129 Kroeker, K.J., Sanford, E., Jellison, B.M., Gaylord, B., 2014. Predicting the effects of ocean
1130 acidification on predator-prey interactions: a conceptual framework based on coastal molluscs.
1131 The Biological Bulletin 226, 211-222.

1132 Kurihara, H., 2008. Effects of CO₂-driven ocean acidification on the early developmental stages
1133 of invertebrates. Marine Ecology Progress Series 373, 275-284.

1134 Kurihara, H., Kato, S., Ishimatsu, A., 2007. Effects of increased seawater pCO₂ on early
1135 development of the oyster *Crassostrea gigas*. Aquatic Biology 1, 91-98.

1136 Kwon, H.-B., Lee, C.-W., Jun, B.-S., Yun, J.-d., Weon, S.-Y., Koopman, B., 2004. Recycling waste
1137 oyster shells for eutrophication control. Resources, Conservation and Recycling 41, 75-82.

1138 La Peyre, M.K., Humphries, A.T., Casas, S.M., La Peyre, J.F., 2014. Temporal variation in
1139 development of ecosystem services from oyster reef restoration. Ecological Engineering 63,
1140 34-44.

1141 Lacoue-Labarthe, T., Nunes, P.A.L.D., Ziveri, P., Cinar, M., Gazeau, F., Hall-Spencer, J.M., Hilmi, N.,
1142 Moschella, P., Safa, A., Sauzade, D., Turley, C., 2016. Impacts of ocean acidification in a
1143 warming Mediterranean Sea: An overview. Regional Studies in Marine Science 5, 1-11.

1144 Lannig, G., Eilers, S., Portner, H.O., Sokolova, I.M., Bock, C., 2010. Impact of ocean acidification
 1145 on energy metabolism of oyster, *Crassostrea gigas*-changes in metabolic pathways and
 1146 thermal response. *Marine Drugs* 8, 2318-2339.
 1147 LDWF, 2004. Louisiana's oyster shell recovery pilot project. Louisiana Department of Wildlife
 1148 and Fisheries. Socioeconomics Research and Development Section and Marine Fisheries
 1149 Division.
 1150 Lee, C.H., Lee do, K., Ali, M.A., Kim, P.J., 2008. Effects of oyster shell on soil chemical and
 1151 biological properties and cabbage productivity as a liming materials. *Waste Management* 28,
 1152 2702-2708.
 1153 Lee, I., Arcodia, C., 2011. The role of regional food festivals for destination branding.
 1154 *International Journal of Tourism Research* 13, 355-367.
 1155 Lee, S. W., Park, S.-B., Jeong, S.-K., Lim, K.-S., Lee, S.-H., Trachtenberg, M.C., 2010. On carbon
 1156 dioxide storage based on biomineralization strategies. *Micron* 41, 273-282.
 1157 Lee, S.W., Hong, S.M., Choi, C.S., 2006. Characteristics of calcification processes in embryos and
 1158 larvae of the Pacific oyster, *Crassostrea gigas*. *Bulletin of Marine Science* 78, 309-317.
 1159 Li, S., Liu, Y., Liu, C., Huang, J., Zheng, G., Xie, L., Zhang, R., 2015. Morphology and classification
 1160 of hemocytes in *Pinctada fucata* and their responses to ocean acidification and warming. *Fish*
 1161 *and Shellfish Immunology*.
 1162 Li, Y., Qin, J.G., Li, X., Benkendorff, K., 2009. Spawning-dependent stress response to food
 1163 deprivation in Pacific oyster *Crassostrea gigas*. *Aquaculture* 286, 309-317.
 1164 Lipton, D., 2004. The value of improved water quality to Chesapeake Bay boaters. *Mar Resour*
 1165 *Econ* 19, 265-270.
 1166 Mac Con Iomaire, M., 2006. A history of seafood in Irish cuisine and culture, *Wild Food:*
 1167 *Proceedings of the Oxford Symposium on Food and Cookery*, 2004. Oxford Symposium.

1168 Matozzo, V., Chinellato, A., Munari, M., Finos, L., Bressan, M., Marin, M.G., 2012. First evidence
 1169 of immunomodulation in bivalves under seawater acidification and increased temperature.
 1170 PloS One 7, e33820.

1171 MEA, 2005. Millenium Ecosystem Assessment. Ecosystems and human well-being: wetlands and
 1172 water. World Resources Institute, Washington, DC.

1173 Meyer, D.L., Townsend, E.C., Thayer, G.W., 1997. Stabilization and erosion control value of
 1174 oyster cultch for intertidal marsh. Restoration Ecology 5, 93-99.

1175 Michener, W.K., Blood, E.R., Bildstein, K.L., Brinson, M.M., Gardner, L.R., 1997. Climate change,
 1176 hurricanes and tropical storms, and rising sea level in coastal wetlands. Ecological Applications
 1177 7, 770-801.

1178 Milazzo, M., Rodolfo-Metalpa, R., Chan, V.B., Fine, M., Alessi, C., Thiyagarajan, V., Hall-Spencer,
 1179 J.M., Chemello, R., 2014. Ocean acidification impairs vermetid reef recruitment. Science
 1180 Report 4, 4189.

1181 Moore, C.C., 2011. Welfare impacts of ocean acidification: an integrated assessment model of
 1182 the US mollusk fishery. National Center for Environmental Economics Working Paper, 11-06.

1183 Moreira, A., Figueira, E., Soares, A.M.V.M., Freitas, R., 2016. The effects of arsenic and seawater
 1184 acidification on antioxidant and biomineralization responses in two closely related Crassostrea
 1185 species. Science of The Total Environment 545–546, 569-581.

1186 Narita, D., Rehdanz, K., 2016. Economic impact of ocean acidification on shellfish production in
 1187 Europe. Journal of Environmental Planning and Management, 1-19.

1188 Narita, D., Rehdanz, K., Tol, R.S., 2012. Economic costs of ocean acidification: a look into the
 1189 impacts on global shellfish production. Climatic Change 113, 1049-1063.

1190 National Research Council, 2004. Non-native oysters in the Chesapeake Bay. Committee on non-
 1191 native oysters in the Chesapeake Bay, Ocean Studies Board, Division on Earth and Life Studies.

1192 Nelson, K.A., Leonard, L.A., Posey, M.H., Alphin, T.D., Mallin, M.A., 2004. Using transplanted
 1193 oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: a pilot study.
 1194 Journal of Experimental Marine Biology and Ecology 298, 347-368.
 1195 Newell, R.I., 2004. Ecosystem influences of natural and cultivated populations of suspension-
 1196 feeding bivalve molluscs: a review. Journal of Shellfish Research 23, 51-62.
 1197 Newell, R.I.E., Fisher, T.R., Holyoke, R.R., Cornwell, J.C., 2005. Influence of Eastern oysters on
 1198 nitrogen and phosphorus regeneration in Chesapeake Bay, USA, in: Dame, R., Olenin, S. (Eds.),
 1199 The Comparative Roles of Suspension-Feeders in Ecosystems. Springer Netherlands, pp. 93-120.
 1200 Ok, Y., Oh, S.-E., Ahmad, M., Hyun, S., Kim, K.-R., Moon, D., Lee, S., Lim, K., Jeon, W.-T., Yang, J.,
 1201 2010. Effects of natural and calcined oyster shells on Cd and Pb immobilization in
 1202 contaminated soils. Environ Earth Sci 61, 1301-1308.
 1203 Paerl, H.W., Pinckney, J.L., Fear, J.M., Peierls, B.L., 1998. Ecosystem responses to internal and
 1204 watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse River
 1205 Estuary, North Carolina, USA. Marine Ecology Progress Series 166, 17-25.
 1206 Pandolfi, J.M., Connolly, S.R., Marshall, D.J., Cohen, A.L., 2011. Projecting coral reef futures
 1207 under global warming and ocean acidification. Science 333, 418-422.
 1208 Panelli, R., Allen, D., Ellison, B., Kelly, A., John, A., Tipa, G., 2008. Beyond Bluff oysters? Place
 1209 identity and ethnicity in a peripheral coastal setting. Journal of Rural Studies 24, 41-55.
 1210 Paolisso, M., Dery, N., 2010. A cultural model assessment of oyster restoration alternatives for
 1211 the Chesapeake Bay. Human Organization 69, 169-179.
 1212 Parker, L.M., O'Connor, W.A., Raftos, D.A., Portner, H.O., Ross, P.M., 2015. Persistence of
 1213 positive carryover effects in the oyster, *Saccostrea glomerata*, following transgenerational
 1214 exposure to ocean acidification. PloS One 10, e0132276.
 1215 Parker, L.M., Ross, P.M., O'Connor, W.A., 2009. The effect of ocean acidification and
 1216 temperature on the fertilization and embryonic development of the Sydney rock oyster
 1217 *Saccostrea glomerata* (Gould 1850). Global Change Biology 15, 2123-2136.

1218 Parker, L.M., Ross, P.M., O'Connor, W.A., Borysko, L., Raftos, D.A., Pörtner, H.-O., 2012. Adult
1219 exposure influences offspring response to ocean acidification in oysters. *Global Change Biology*
1220 18, 82-92.

1221 Parker, L.M., Ross, P.M., O'Connor, W.A., Portner, H.O., Scanes, E., Wright, J.M., 2013. Predicting
1222 the response of molluscs to the impact of ocean acidification. *Biology 2*, 651-692.

1223 Parker, L.M., Ross, P.M., O'Connor, W.A., 2010. Comparing the effect of elevated $p\text{CO}_2$ and
1224 temperature on the fertilization and early development of two species of oysters. *Marine*
1225 *Biology* 157, 2435-2452.

1226 Parker, L.M., Ross, P.M., O'Connor, W.A., 2011. Populations of the Sydney rock oyster,
1227 *Saccostrea glomerata*, vary in response to ocean acidification. *Marine Biology* 158, 689-697.

1228 Pechenik, J.A., 2006. Larval experience and latent effects-metamorphosis is not a new beginning.
1229 *Integrative and Comparative Biology* 46, 323-333.

1230 Pechenik, J.A., Wendt, D.E., Jarrett, J.N., 1998. Metamorphosis is not a new beginning.
1231 *Bioscience*, 901-910.

1232 Peterson, C.H., Grabowski, J.H., Powers, S.P., 2003. Estimated enhancement of fish production
1233 resulting from restoring oyster reef habitat: quantitative valuation. *Marine Ecology Progress*
1234 *Series* 264, 249-264.

1235 Peterson, C.H., Lipcius, R.N., 2003. Conceptual progress towards predicting quantitative
1236 ecosystem benefits of ecological restorations. *Marine Ecology Progress Series* 264, 297-307.

1237 Piehler, M.F., Smyth, A.R., 2011. Habitat-specific distinctions in estuarine denitrification affect
1238 both ecosystem function and services. *Ecosphere* 2, art12.

1239 Pörtner, H., 2008. Ecosystem effects of ocean acidification in times of ocean warming: a
1240 physiologist's view. *Marine Ecology Progress Series* 373, 203-217.

1241 Pörtner, H., Langenbuch, M., Reipschläger, A., 2004. Biological impact of elevated ocean CO_2
1242 concentrations: lessons from animal physiology and Earth history. *Journal of Oceanography* 60,
1243 705-718.

1244 Przeslawski, R., Byrne, M., Mellin, C., 2014. A review and meta-analysis of the effects of multiple
1245 abiotic stressors on marine embryos and larvae. *Global Change Biology*.

1246 Range, P., Piló, D., Ben-Hamadou, R., Chícharo, M.A., Matias, D., Joaquim, S., Oliveira, A.P.,
1247 Chícharo, L., 2012. Seawater acidification by CO₂ in a coastal lagoon environment: Effects on
1248 life history traits of juvenile mussels *Mytilus galloprovincialis*. *Journal of Experimental Marine*
1249 *Biology and Ecology* 424-425, 89-98.

1250 Richards, G.P., Watson, M.A., Needleman, D.S., Church, K.M., Hase, C.C., 2015a. Mortalities of
1251 Eastern and Pacific oyster larvae caused by the pathogens *Vibrio coralliilyticus* and *Vibrio*
1252 *tubishii*. *Appl Environ Microb* 81, 292-297.

1253 Richards, R.G., Davidson, A.T., Meynecke, J.-O., Beattie, K., Hernaman, V., Lynam, T., van Putten,
1254 I.E., 2015b. Effects and mitigations of ocean acidification on wild and aquaculture scallop and
1255 prawn fisheries in Queensland, Australia. *Fisheries Research* 161, 42-56.

1256 Ries, J.B., Cohen, A.L., McCorkle, D.C., 2009. Marine calcifiers exhibit mixed responses to CO₂-
1257 induced ocean acidification. *Geology* 37, 1131-1134.

1258 Rodolfo-Metalpa, R., Houlbreque, F., Tambutte, E., Boisson, F., Baggini, C., Patti, F.P., Jeffree, R.,
1259 Fine, M., Foggo, A., Gattuso, J.P., Hall-Spencer, J.M., 2011. Coral and mollusc resistance to
1260 ocean acidification adversely affected by warming. *Nature Climate Change* 1, 308-312.

1261 Rodrigues, L.C., van den Bergh, J.C.J.M., Ghermandi, A., 2013. Socio-economic impacts of ocean
1262 acidification in the Mediterranean Sea. *Marine Policy* 38, 447-456.

1263 Rodríguez-Romero, A., Jarrold, M.D., Massamba-N'Siala, G., Spicer, J.I., Calosi, P., 2015. Multi-
1264 generational responses of a marine polychaete to a rapid change in seawater pCO₂.
1265 *Evolutionary Applications*.

1266 Ross, P.M., Parker, L., O'Connor, W.A., Bailey, E.A., 2011. The impact of ocean acidification on
1267 reproduction, early development and settlement of marine organisms. *Water* 3, 1005-1030.

1268 Rossoll, D., Bermudez, R., Hauss, H., Schulz, K.G., Riebesell, U., Sommer, U., Winder, M., 2012.

1269 Ocean acidification-induced food quality deterioration constrains trophic transfer. *PloS One* 7,

1270 e34737.

1271 Rumrill, S.S., 1990. Natural mortality of marine invertebrate larvae. *Ophelia* 32, 163-198.

1272 Rusher, K., 2003. The Bluff Oyster Festival and regional economic development: festivals as

1273 culture commodified. *Food tourism around the world: Development, management and*

1274 *markets*, 192-205.

1275 Sanford, E., Gaylord, B., Hettinger, A., Lenz, E.A., Meyer, K., Hill, T.M., 2014. Ocean acidification

1276 increases the vulnerability of native oysters to predation by invasive snails. *P Roy Soc B-Biol Sci*

1277 281, 20132681.

1278 Schmitt, L.H., Brugere, C., 2013. Capturing ecosystem services, stakeholders' preferences and

1279 trade-offs in coastal aquaculture decisions: a Bayesian belief network application. *PloS One* 8,

1280 e75956.

1281 Schneider, D.W., Stoeckel, J.A., Rehmann, C.R., Douglas Blodgett, K., Sparks, R.E., Padilla, D.K.,

1282 2003. A developmental bottleneck in dispersing larvae: implications for spatial population

1283 dynamics. *Ecology Letters* 6, 352-360.

1284 Scott, M., Hull, S., Mullenhoff, P., 1971. The calcium requirements of laying hens and effects of

1285 dietary oyster shell upon egg shell quality. *Poultry Science* 50, 1055-1063.

1286 Scyphers, S.B., Picou, J.S., Brumbaugh, R.D., Powers, S.P., 2014. Integrating societal perspectives

1287 and values for improved stewardship of a coastal ecosystem engineer. *Ecology and Society* 19.

1288 Scyphers, S.B., Powers, S.P., Heck, K.L., Jr., Byron, D., 2011. Oyster reefs as natural breakwaters

1289 mitigate shoreline loss and facilitate fisheries. *PloS One* 6, e22396.

1290 Seijo, J.C., Villanueva-Poot, R., Charles, A., 2016. Bioeconomics of ocean acidification effects on

1291 fisheries targeting calcifier species: A decision theory approach. *Fisheries Research* 176, 1-14.

1292 Simkiss, K., Wilbur, K.M., 2012. *Biomineralization*. Elsevier.

1293 Small, D., Calosi, P., White, D., Spicer, J.I., Widdicombe, S., 2010. Impact of medium-term
 1294 exposure to CO₂ enriched seawater on the physiological functions of the velvet swimming crab
 1295 *Necora puber*. *Aquatic Biology* 10, 11-21.

1296 Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization and
 1297 genetic adaptation will determine 'winners' and 'losers'. *The Journal of Experimental Biology*
 1298 213, 912-920.

1299 Soto, D., Aguilar-Manjarrez, J., Brugère, C., Angel, D., Bailey, C., Black, K., Edwards, P., Costa-
 1300 Pierce, B., Chopin, T., Deudero, S., 2008. Applying an ecosystem-based approach to
 1301 aquaculture: principles, scales and some management measures, in: Soto D, A.-M.J.,
 1302 Hishamunda N (Ed.), *Building an ecosystem approach to aquaculture*. FAO Fisheries and
 1303 Aquaculture Proceedings No. 14. Rome, Italy: Food and Agriculture Organization, pp. 15–35.

1304 Stenzel, H.B., 1964. Oysters: Composition of the larval shell. *Science* 145, 155-156.

1305 Stocker, T., Qin, D., Plattner, G., Tignor, M., Allen, S., Boschung, J., Nauels, A., Xia, Y., Bex, B.,
 1306 Midgley, B., 2013. IPCC, 2013: Climate change 2013: the physical science basis. Contribution of
 1307 working group I to the fifth assessment report of the intergovernmental panel on climate
 1308 change.

1309 Sui, Y., Kong, H., Huang, X., Dupont, S., Hu, M., Storch, D., Portner, H.O., Lu, W., Wang, Y., 2016.
 1310 Combined effects of short-term exposure to elevated CO₂ and decreased O₂ on the physiology
 1311 and energy budget of the thick shell mussel *Mytilus coruscus*. *Chemosphere* 155, 207-216.

1312 Sunday, J.M., Calosi, P., Dupont, S., Munday, P.L., Stillman, J.H., Reusch, T.B., 2014. Evolution in
 1313 an acidifying ocean. *Trends in Ecology and Evolution* 29, 117-125.

1314 Tahil, A.S., Dy, D.T., 2016. Effects of reduced pH on the early larval development of hatchery-
 1315 reared Donkey's ear abalone, *Haliotis asinina* (Linnaeus 1758). *Aquaculture*.

1316 Talmage, S.C., Gobler, C.J., 2009. The effects of elevated carbon dioxide concentrations on the
 1317 metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops

1318 (*Argopecten irradians*), and Eastern oysters (*Crassostrea virginica*). Limnology and
 1319 Oceanography 54, 2072-2080.
 1320 Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., This issue. The role of kelp species as biogenic
 1321 habitat formers in coastal marine ecosystems. J Exp Mar Biol Ecol.
 1322 Thompson, E.L., O'Connor, W., Parker, L., Ross, P., Raftos, D.A., 2015. Differential proteomic
 1323 responses of selectively bred and wild Sydney rock oyster populations exposed to elevated CO₂.
 1324 Molecular Ecology 24(6), pp.1248-1262.
 1325 Thomsen, J., Casties, I., Pansch, C., Kortzinger, A., Melzner, F., 2012. Food availability outweighs
 1326 ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. Global
 1327 change biology 19, 1017-1027.
 1328 Thomsen, J., Gutowska, M.A., Saphörster, J., Heinemann, A., Trübenbach, K., Fietzke, J.,
 1329 Hiebenthal, C., Eisenhauer, A., Körtzinger, A., Wahl, M., Melzner, F., 2010. Calcifying
 1330 invertebrates succeed in a naturally CO₂-rich coastal habitat but are threatened by high levels
 1331 of future acidification. Biogeosciences 7, 3879-3891.
 1332 Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological
 1333 Reviews 25, 1-45.
 1334 Timmins-Schiffman, E., O'Donnell, M.J., Friedman, C.S., Roberts, S.B., 2012. Elevated pCO₂
 1335 causes developmental delay in early larval Pacific oysters, *Crassostrea gigas*. Marine Biology
 1336 160, 1973-1982.
 1337 Tolley, S.G., Volety, A.K., 2005. The role of oysters in habitat use of oyster reefs by resident
 1338 fishes and decapod crustaceans. Journal of Shellfish Research 24, 1007-1012.
 1339 Tunnicliffe, V., Davies, K.T.A., Butterfield, D.A., Embley, R.W., Rose, J.M., Chadwick Jr, W.W.,
 1340 2009. Survival of mussels in extremely acidic waters on a submarine volcano. Nature
 1341 Geoscience 2, 344-348.
 1342 UNEP, 2010. UNEP Emerging Issues: Environmental Consequences of Ocean Acidification: A
 1343 Threat to Food Security. UNEP.

1344 Uthicke, S., Logan, M., Liddy, M., Francis, D., Hardy, N., Lamare, M., 2015. Climate change as an
 1345 unexpected co-factor promoting coral eating seastar (*Acanthaster planci*) outbreaks. Scientific
 1346 Reports 5, 8402.

1347 Videla, J., Chaparro, O., Thompson, R., Concha, I., 1998. Role of biochemical energy reserves in
 1348 the metamorphosis and early juvenile development of the oyster *Ostrea chilensis*. Marine
 1349 Biology 132, 635-640.

1350 Visser, M.E., 2008. Keeping up with a warming world; assessing the rate of adaptation to climate
 1351 change. P Roy Soc B-Biol Sci 275, 649-659.

1352 Volety, A.K., Haynes, L., Goodman, P., Gorman, P., 2014. Ecological condition and value of oyster
 1353 reefs of the Southwest Florida shelf ecosystem. Ecological Indicators 44, 108-119.

1354 Waldbusser, G.G., Steenson, R.A., Green, M.A., 2011a. Oyster shell dissolution rates in estuarine
 1355 waters: effects of pH and shell legacy. Journal of Shellfish Research 30, 659-669.

1356 Waldbusser, G.G., Voigt, E.P., Bergschneider, H., Green, M.A., Newell, R.I.E., 2011b.
 1357 Biocalcification in the Eastern oyster (*Crassostrea virginica*) in relation to long-term trends in
 1358 Chesapeake Bay pH. Estuaries and Coasts 34, 221-231.

1359 Walles, B., Mann, R., Ysebaert, T., Troost, K., Herman, P.M.J., Smaal, A.C., 2015. Demography of
 1360 the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef
 1361 persistence. Estuarine, Coastal and Shelf Science 154, 224-233.

1362 Wang, Q., Cao, R., Ning, X., You, L., Mu, C., Wang, C., Wei, L., Cong, M., Wu, H., Zhao, J., 2016.
 1363 Effects of ocean acidification on immune responses of the Pacific oyster *Crassostrea gigas*. Fish
 1364 & Shellfish Immunology 49, 24-33.

1365 Watson, S.-A., Southgate, P.C., Tyler, P.A., Peck, L.S., 2009. Early larval development of the
 1366 Sydney rock oyster *Saccostrea glomerata* under near-future predictions of CO₂-driven ocean
 1367 acidification. Journal of Shellfish Research 28, 431-437.

1368 Wedepohl, K.H., Baumann, A., 2000. The use of marine molluskan shells for roman glass and
 1369 local raw glass production in the Eifel Area (Western Germany). *Naturwissenschaften* 87, 129-
 1370 132.

1371 Weiner, S., Addadi, L., 2002. Calcium carbonate formation in biology: the involvement of an
 1372 amorphous calcium carbonate precursor phase. *Geochimica et Cosmochimica Acta* 66, A827.

1373 Weiss, I.M., Tuross, N., Addadi, L., Weiner, S., 2002. Mollusc larval shell formation: amorphous
 1374 calcium carbonate is a precursor phase for aragonite. *Journal of Experimental Zoology* 293,
 1375 478-491.

1376 Welladsen, H.M., Southgate, P.C., Heimann, K., 2010. The effects of exposure to near-future
 1377 levels of ocean acidification on shell characteristics of *Pinctada fucata* (Bivalvia: Pteriidae).
 1378 *Molluscan Research* 30, 125.

1379 White, L.J., Koss, R.S., Knights, A.M., Eriksson, A., Robinson, L.A., 2013. ODEMM Linkage
 1380 Framework Userguide (Version 2). ODEMM Guidance Document Series No.3. EC FP7 project
 1381 (244273) 'Options for Delivering Ecosystem-based Marine Management'. University of
 1382 Liverpool. ISBN: 978-0- 906370-87-6: 14 pp.

1383 Wingard, G.L., Lorenz, J.J., 2014. Integrated conceptual ecological model and habitat indices for
 1384 the southwest Florida coastal wetlands. *Ecological Indicators* 44, 92-107.

1385 Wright, J.M., Parker, L.M., O'Connor, W.A., Williams, M., Kube, P., Ross, P.M., 2014. Populations
 1386 of Pacific oysters *Crassostrea gigas* respond variably to elevated CO₂ and predation by *Morula*
 1387 *marginalba*. *The Biological Bulletin* 226, 269-281.

1388 Yang, E.-I., Kim, M.-Y., Park, H.-G., Yi, S.-T., 2010. Effect of partial replacement of sand with dry
 1389 oyster shell on the long-term performance of concrete. *Construction and Building Materials* 24,
 1390 758-765.

1391 Yang, E.-I., Yi, S.-T., Leem, Y.-M., 2005. Effect of oyster shell substituted for fine aggregate on
 1392 concrete characteristics: Part I. Fundamental properties. *Cement Concrete Res* 35, 2175-2182.

1393 Yao, Z., Xia, M., Li, H., Chen, T., Ye, Y., Zheng, H., 2014. Bivalve shell: not an abundant useless
1394 waste but a functional and versatile biomaterial. *Critical Reviews in Environmental Science and*
1395 *Technology* 44, 2502-2530.

1396 Yoon, G.-L., Kim, B.-T., Kim, B.-O., Han, S.-H., 2003. Chemical–mechanical characteristics of
1397 crushed oyster-shell. *Waste Management* 23, 825-834.

1398 Yoon, H., 2004. Oyster shell as substitute for aggregate in mortar. *Waste Management Research*
1399 22, 158-170.

1400 zu Ermgassen, P.S.E., Spalding, M.D., Grizzle, R.E., Brumbaugh, R.D., 2013. Quantifying the loss
1401 of a marine ecosystem service: filtration by the Eastern oyster in US estuaries. *Estuaries and*
1402 *Coasts* 36, 36-43.

1403

1404 Table 1 (web version (colour); print (grayscale)): Ecosystem goods and services provided by oysters and oyster reefs, following the
 1405 ODEMM Linkage Framework description (White et al., 2013), and the potential impacts of ocean acidification (OA). '✓' indicates that
 1406 the service is provided by oysters, '✗' indicates the service is not provided (according to the available literature). Direction of arrows
 1407 indicates expected change in the ecosystem service (i.e. ↑ indicates increase in ES provision, ↓ a decrease in ES provision). '~'
 1408 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	✗	✗	✗
	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	✓ (<i>shell collection</i>)	~\$13m ⁻³ (Lemasson, unpublished)	Yes ↓~
Regulating	Air purification	X	X	X
	Climate regulation (incl. carbon sequestration)	✓ (<i>carbon sequestration</i>)	Unknown	Yes ↓~
	Disturbance prevention or moderation	✓	Upward of \$6 million (<i>for coastal defence structures- Firth et al., 2014</i>)	Yes ↓~
	Regulation of water flows	X	X	X
	Waste treatment (esp. water purification)	✓ (<i>water purification, Chl-a removal, nutrient cycling</i>)	\$1385-\$6716/yr/ha. (Grabowski et al., 2012) \$314 836/yr (<i>Newell et al., 2005</i>) \$18 135/million oysters (<i>Kasperski and Wieland, 2009</i>) \$3000/ac./yr (<i>Piehlner and Smyth, 2011</i>) \$293 993/yr (<i>Beseres-Pollack et al., 2013</i>)	Yes ↓~
	Coastal erosion prevention	✓ (<i>shoreline stabilization, erosion prevention</i>)	Upward of \$6 million for coastal defence structures (<i>Firth et al. 2014</i>)	Yes ↓~
	Biological control	✓ (<i>facilitate submerged aquatic vegetation</i>)	Unknown	Yes ↓~
Cultural	Aesthetic information	X	X	X
	Recreation & leisure	✓	\$222 million (<i>U.S. National Research Council, 2004</i>)	Yes ↓~
	Inspiration for culture, art and design	X	X	X
	Spiritual experience	✓ (<i>assumed</i>)	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/)).

1429 Figure 2: (web version)

1430

1431

1432

1433 Figure 2: (print version)

1434

1435 Figure 3: (web version)

1436

1437 Figure 3: (print version)

1438

Present day

Future ocean acidification scenario

1440

1441

1442

1443

1444 **Highlights:**

- 1445 • Ocean acidification (OA) threatens all stages of the life-cycle of oysters.
- 1446 • Oyster reefs provide numerous ecosystem services (ES)
- 1447 • The delivery of ESs associated with healthy oyster reefs may be threatened
- 1448 by OA.
- 1449 • Further studies linking OA and ES are urgently needed.