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Monograph

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

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ABSTRACT

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

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1. Introduction

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

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

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

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

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

2. The biological impacts of ocean acidification on oysters

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

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

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

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

OA can also affect development rates. Multi-stressor experiments manipulating pCO_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., 2012, 2013a; Parker et al., 2009, 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).