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Ocean acidification and marine microorganisms: responses and consequences☆

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Summary Ocean acidification (OA) is one of the global issues caused by rising atmospheric CO_2. The rising pCO_2 and resulting pH decrease has altered ocean carbonate chemistry. Microbes are key components of marine environments involved in nutrient cycles and carbon flow in marine ecosystems. However, these marine microbes and the microbial processes are sensitive to ocean pH shift. Thus, OA affects the microbial diversity, primary productivity and trace gases emission in oceans. Apart from that, it can also manipulate the microbial activities such as quorum sensing, extracellular enzyme activity and nitrogen cycling. Short-term laboratory experiments, mesocosm studies and changing marine diversity scenarios have illustrated undesirable effects of OA on marine microorganisms and ecosystems. However, from the microbial perspective, the current understanding on effect of OA is based mainly on limited experimental studies. It is challenging to predict response of marine microbes based on such experiments for this complex process. To study the response of marine microbes towards OA, multiple approaches should be implemented by using functional genomics, new generation microscopy, small-scale interaction among organisms and/or between organic matter and organisms. This review focuses on the response of marine microorganisms to OA and the experimental approaches to investigate the effect of changing ocean carbonate chemistry on microbial mediated processes.

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1. Introduction

Human activities such as burning of fossil fuels and industrialization have resulted in rising atmospheric CO_2 concentration. Emission of CO_2 causing increasing concentration of CO_2 in the atmosphere is one of the major drivers of global warming as well as seawater carbonate chemistry. Oceans play a very important role in the global carbon cycle and Earth's climate system (Chavez et al., 2011). The uptake of anthropogenic CO_2 from the atmosphere by ocean physics and biology has already led to substantial changes in the ocean carbon cycle, with potentially larger changes looming ahead (Reid et al., 2009; Takahashi et al., 2012). Oceans act as a reservoir for CO_2 and there is a flux of CO_2 across the interface between the atmosphere and ocean surface. Uptake of CO_2 by the ocean is an essential buffering process of seawater, however, it also alters the chemistry of the seawater at a fundamental level. Increase of CO_2 in the ocean and a decline in ocean pH, thus, promoting one of the most critical events known as ocean acidification (OA) (Raven, 2005). The average ocean surface water pH has fallen by approximately 0.1 unit over about the past 200 years (Raven, 2005) and is expected to decrease a further 0.3—0.4 unit if atmospheric CO_2 concentrations reach 800 ppmv (Orr et al., 2005) against the present concentration of 397 ppmv. The subsequent impact of OA on marine life has become one of the most important issues. The chemical changes that occur when CO_2 is absorbed by the ocean result in formation of carbonic acid which decreases seawater pH, carbonate ion concentration and calcium carbonate saturation (Lohbeck et al., 2012). Maintenance of appropriate carbonate ion saturation is essential for the formation of calcium carbonate, which is the basic building block of skeletons and shells of a large number of marine organisms, including corals, shellfish and plankton (Doney et al., 2009a; Hoegh-Guldberg et al., 2007).

The marine environment covers more than 70% of the total earth surface, which encompasses a diverse set of habitats ranging from tropical, shallow water coral-reef to deep ocean trenches. Within these habitats, millions of organisms survive which include many autotrophs, animals and both autotrophic and heterotrophic microorganisms (Dash et al., 2013; Pomeroy et al., 2007). The impact of OA has been extensively studied in calcifying marine organisms to understand the impact on calcification process. However, the consequences of OA also affect the marine microorganisms that are responsible for the net productivity of the ocean. Microbes are key component of marine biogeochemical cycles which are involved in nutrient cycles, organic matter decomposition and carbon flow in the marine ecosystem (Arnosti, 2011; Azam and Malfatti, 2007). So far, deleterious effects of OA have not been studied in marine microbes in detail, although, OA is modulating many crucial activities of microbes (such as N_2 fixation, primary production, trace gas emission and extracellular enzyme activities). This review discusses the effect of OA on ocean carbonate chemistry and marine microbially-mediated processes. It also covers the experimental models and approaches that can be used to study the response of marine microbes towards changing ocean chemistry.

2. Chemistry of ocean acidification: ocean carbonate system

A series of chemical reactions control seawater carbonate chemistry, which in turn interacts with atmospheric pCO_2. The ocean acts as a sink of CO_2 and once dissolved in seawater, CO_2 reacts with water to form carbonic acid (H_2CO_3). However, ocean stores CO_2 as dissolved inorganic carbon (DIC) which remains in the form of dissolved CO_2 and H_2CO_3 (1%) while the rest is in the form of HCO_3^- (~90%) and CO_3^{2-} (~9%) (Brewer, 1997; Rost et al., 2008; Wolf-Gladrow et al., 1999). Adding CO_2 to seawater, thus increase HCO_3^- that bring about a decrease in ocean water pH by increasing H^+ concentration. Carbonic acid is a weak acid that dissociates into hydrogen ions and bicarbonate ions. The additional hydrogen ions combine with carbonate ions to form bicarbonate ions (Doney et al., 2009a, 2009b).

$$[CO_2] + [H_2O] \rightarrow [H_2CO_3],$$

$$[H_2CO_3] \rightarrow [H^+] + [HCO_3^-],$$

$$[H^+] + [CO_3^{2-}] \rightarrow [HCO_3^-].$$

Changing CO_2 will affect numerous aspects of seawater chemistry. OA is not just a single problem associated with rising CO_2 but it will modify many biochemical cycles and functioning of organisms (Solomon et al., 2009). Thus, with an increase in the atmospheric level of CO_2, there will be a subsequent increase in the concentration of CO_2 in the surface oceans. Carbon dioxide in the seawater takes part in several biological and geological reactions, but this gas is chemically very much inactive in atmosphere. At present, the pCO_2 has reached about 380 μatm and is expected to rise to 750 μatm by the end of this century (Beaufort et al., 2011; Solomon et al., 2009) or even values >1000 μatm which will lead to more extreme changes in seawater pH (Raupach et al., 2007; Raven, 2005).

It has been projected that there will be a decline in average pH from 8.1 to 7.8 and this projected pH drop (0.3—0.4) by the end of this century is equivalent to approximately 150% increase in H^+ and 50% decrease in CO_3^{2-} concentrations (Orr et al., 2005). The penalty of elevated atmospheric CO_2 is not only limited to decline in pH but also affects carbonate ion concentration that could further impact on the calcification process for marine organisms in building carbonate shells (Abbasi and Abbasi, 2011; Berelson et al., 2007). Bicarbonate and calcium ion together participate during the process of calcification. For the formation of calcium carbonate in biological materials, HCO_3^- is required; therefore, it is the challenge of overcoming enhanced dissolution (due to the decreased CO_3^{2-} level) for calcifying organisms. The decrease in CO_3^{2-} concentrations will affect calcium carbonate saturation (Ω), i.e. ratio of the ion activity product to the stoichiometric solubility product. If saturation is equal to unity, then solid and solution are in a state of equilibrium. If $\Omega < 1$ then dissolution of calcium carbonate can occur because of under-saturation and $\Omega > 1$ facilitates precipitation of calcium carbonate (a supersaturated state). A positive correlation between saturated state and calcium carbonate production rate has also been reported in warm water corals (Gattuso et al., 1998; Guinotte and Fabry, 2008). Calcite and aragonite are two common polymorphs of calcium carbonate. Solubility of aragonite is higher than calcite. As a result, calcifiers which produce aragonite are more susceptible to OA or calcium carbonate saturation (McCulloch et al., 2012; Yool et al., 2013). As the calcifiers are more prone to changes in carbonate chemistry, but fluctuation in ocean carbonate chemistry and calcifying organism community structure will affect the overall marine ecosystem.

3. Effect of change in carbonate chemistry on marine ecosystem: an overview

OA has ambivalent effects on marine organisms, biogeochemical cycle and ecosystems, which is supported by number of recent studies (Archer et al., 2013; Fabry et al., 2008; Kaplan et al., 2013). However, the understanding of the problem due to OA is still at its beginning. OA will be prolonged in the near future as a serious environmental peril (Brewer, 2013; Caldeira and Wickett, 2003). Decline in ocean water pH is a slow process and it is difficult to recognize how precisely minute pH shift can influence marine ecosystem. Various researches have highlighted the biological effects of OA on acute pH shifts rather than understating slow and continuous pH swings on global pH changes. However, looking at the ocean carbonate cycle, significant effects on calcifying organisms and phytoplankton are expected (Gattuso et al., 1999) and the changes will certainly affect the ocean productivity and the carbonate chemistry (Gutowska et al., 2008; Iglesias-Rodriguez et al., 2008).

Coral reefs, which are a symbol of diverse, biologically active marine ecosystems of economic value, occur mostly in well-lit and shallow waters (Kennedy et al., 2002; Spalding et al., 2001) and scarcely in cold and deep-waters (Turley et al., 2007). In terms of global climate change, reef-building organisms are amid the most sensitive life forms affected by changes in ocean carbonate chemistry. Lowering of calcification rates and coral bleaching are a universal dilemma of OA (Anthony et al., 2008). Studies carried out in simulated mesocosms suggested that the calcification rate of a reef is related to the aragonite saturation (Leclercq et al., 2000). Under most IPCC emission scenarios (IPCC, 2013), corals may unlikely remain abundant and could be rare on tropical and subtropical regions by the middle of this century if CO_2 doubles or triples above present levels.

OA is also believed to have impacts on other aspects of the benthic ecosystem too. The diverse communities of benthic sediments are characteristically occupied by several species at varying depth (Barnes and Hughes, 1988). The discrepancy in pH tolerance of marine community makes it complicated to predict the future due to the requirement of adaptive changes in the marine organisms (Hofmann et al., 2010). Thus, acclimatization and phenotypic plasticity are adaptive responses to changing marine ecosystem, which significantly varies among different groups in the different communities (Hofmann et al., 2013; Shirayama et al., 2004). Though variable and contradictory results have been obtained regarding the effect of OA on coccolithophores, meta-analysis revealed a negative effect of OA on calcification of two most abundant coccolithophore species, i.e. *Emiliania huxleyi* and *Gephyrocapsa oceanica* (Meyer and Riebesell, 2015; Ridgwell et al., 2009).

In the last decade, substantial efforts have been made to measure the climate changes and a number of projects are underway to synthesize them and to put them into the context of climate variability and long-term change. However, experimental advances are required for better understanding. It has been suggested that, enrichment of anthropogenic CO_2 in ocean affects both marine nutrient biogeochemistry as well as microbes mediated nutrient transformations (Hutchins et al., 2009). Primary productivity, bacterial respiration, calcification, carbonate dissolution, trace gas production, trace metal availability, nitrogen cycling and phytoplankton biochemical composition are a few key processes mediated by marine microorganisms and could be susceptible to OA (Joint et al., 2011).

4. Response of marine microorganisms and associated processes to ocean acidification

Enrichment of the ocean with anthropogenic CO_2 and subsequent acidification will have wide consequences on marine biogeochemistry and microorganisms. Fluxes through heterotrophic bacteria and the rest of the microbial loop are likely to be different in a high CO_2 world (Table 1). One possibility is that higher CO_2, lower pH and unusual warming will cause changes in microbial diversity and composition (Joint et al., 2009). Microbially mediated processes are crucial in marine ecosystem functioning. These marine microbes can easily adapt to changing pH, but the resulting modulations on microbially-driven processes are relatively less definite (Fig. 1). Marine microorganisms are responsible for more than 50% of global primary production and play an integral part in major biogeochemical cycles. The extremely abundant and diverse marine microorganisms play a key role in regulation of earth's climate and most importantly the level of CO_2 and CH_4. Thus, OA ultimately affects the marine microbes to alter their physiological role. The key microbial processes affected by OA are discussed below.

4.1. Microbial based primary productivity

Photosynthetic marine organisms supply more than 90% of total organic carbon produced in the sea by fixing CO_2. Cyanobacteria have foremost impact on ocean carbon cycle, as they are the most abundant photosynthetic prokaryotes in marine environment (Burns et al., 2005). In the marine system, about 50% of the fixed carbon is contributed by cyanobacteria (Partensky et al., 1999). Most of the marine photoautotrophs have developed inorganic carbon concentrating mechanisms (CCM) for carbon fixation. CCM is a process by which photosynthetic organisms take up bicarbonate ions (HCO_3^-) to overcome the limited CO_2 concentration. In most of the marine phytoplankton, key carbon fixing enzymes such as ribulose-bisphosphate carboxylase/oxygenase (RUBISCO) have poor affinity towards CO_2 (Daley et al., 2012). Thus, in some marine phytoplankton, low CO_2 level increases the production of RUBISCO while others have evolved RUBISCO with high affinity towards CO_2 to maintain photosynthesis (Koch et al., 2013; Reinfelder, 2011). CCM also assists in maintaining rapid growth under low peripheral DIC

Table 1 Response of marine microorganisms and dependent phenomenon to OA.

Process	Importance	Effect of ocean acidification
Primary productivity	Major influence on global carbon cycle	Elevated pCO_2 can increase photosynthesis rate and cyanobacterial blooms (Eggers et al., 2014; Shetye et al., 2013)
Trace gases emission	Global climate change	Decline in pH can decrease trace gases emission from marine source (Hopkins et al., 2010)
Nitrogen fixation	Nitrogen source to ocean	Effect of pH shift depends on the organism and availability of trace metals N_2 fixation may increase or decrease (Shetye et al., 2013; Shi et al., 2010)
Community composition	Ecological balance	Can considerably transform the community composition of ocean. Thus, affects overall microbial loop (Weinbauer et al., 2011)
Organic matter degradation	Nutrient recycling	Decline in pH increases the polysaccharide and other organic matter degradation (Piontek et al., 2010)
Enzymatic activity	Degradation and recycling	Protease and glucosidase activity decreases at low pH whereas lipase activity declines at elevated pCO_2 (Yamada and Suzumura, 2010)
Quorum sensing	Cell—cell interaction	Increase the growth of pathogenic microbes nearby corals (Generous, 2014)

concentrations (Badger et al., 2006). Extensive studies on the effect of elevated pCO_2 on cyanobacteria suggest the increase in growth of these organisms, e.g. *Synechococcus* sp., *Trichodesmium* sp., *Crocosphaera watsonii* and *Prochlorococcus* sp. (Barcelos e Ramos et al., 2007; Fu et al., 2007; Kranz et al., 2009, 2010). However, decreased growth rate under elevated pCO_2 was also observed in *Nodularia spumigena* (Czerny et al., 2009).

The overall effect of increasing pCO_2 is predominantly on cell division which further affects cellular elemental ratio of C:N or P:N (Barcelos e Ramos et al., 2007; Levitan et al., 2007; Liu et al., 2010). Lomas et al. (2012) studied the response of cyanobacteria in the subtropical North Atlantic and found rapid acclimatization to changing pH/pCO_2. Response to the changing environment in terms of primary productivity is likely to be controlled by other factors such as community structure, changes in other physico-chemical parameters, i.e. nutrients and temperature (Eggers et al., 2014; Kroeker et al., 2013). These variations in response of marine photosynthetic microbial community towards elevated pCO_2 confirm that response towards OA is species specific (Price et al., 2011). This species specificity entails that the action of natural selection could differ among organisms (Collins et al., 2014). Elevated CO_2 and reduced pH levels can interact with solar radiation to affect marine primary producers. Shoaling of the upper mixed layer due to ocean warming and freshening can lead to additional photosynthetically active radiation (PAR) and ultraviolet (UV) exposure, which can increase the photosynthesis or growth of both phytoplankton and macroalgae (Gao et al., 2012). Short-term experiments witnessed a small but significant stimulation of primary production in oceanic environment in response to elevated CO_2 concentration (Hein and Sand-Jensen, 1997). However, the increase in the primary production may lead to the eutrophication and anoxia in surface ocean to affect global nutrient balance in the ocean (Yang et al., 2008).

4.2. Nitrogen fixation

Microbial nitrogen fixation is the major source of nitrogen input into the marine environment. Nitrogen fixation makes new nitrogen available to the marine environment that further supports biological carbon export and sequestration (Sohm et al., 2011). Diazotrophic cyanobacteria in the marine environment fix substantial nitrogen, which includes unicellular cyanobacteria and filamentous cyanobacteria (with and without heterocysts). They are either free living or live in symbiotic relationship with other phototrophs. *Trichodesmium* spp. are major N_2 fixing bacteria in marine environment and contribute about 50% of the total fixed nitrogen of all marine environment (Capone et al., 2005). Although non-cyanobacterial diazotrophs such as chemoautotrophic or heterotrophic diazotrophs also contribute to the marine N_2 fixation in surface seawater, the contribution has been regarded as trivial (Riemann et al., 2010). Most of these non-cyanobacterial diazotrophs have been obtained from open-ocean epipelagic seawater cluster with a wide range of bacterial groups, i.e. *alpha*-, *beta*-, *gamma*- and *delta-proteobacteria* and *Firmicutes* (Moisander et al., 2014). However, little is known regarding the effect of OA on the N_2 fixation ability of these groups of organisms. Short-term studies on *Trichodesmium* spp. reveal that OA or elevated pCO_2 will substantially increase the N_2 fixation (Hutchins et al., 2007; Levitan et al., 2007; Shetye et al., 2013). This enhanced N_2 fixation is due to an increase in the availability of energetic resources for cellular processes under elevated CO_2, which also catalyzes the conversion between CO_2 and HCO_3^- (Kranz et al., 2009, 2010). Conversely, Czerny et al. (2009) reported a decrease in N_2 fixation in the heterocystous cyanobacterium *Nodularia spumigena* at increasing pCO_2 level.

The response to elevated pCO_2 is not only restricted to carbon flux or N_2 fixation. Other nutrient cycles are also affected by OA. Decline in pH of ocean water slows down the

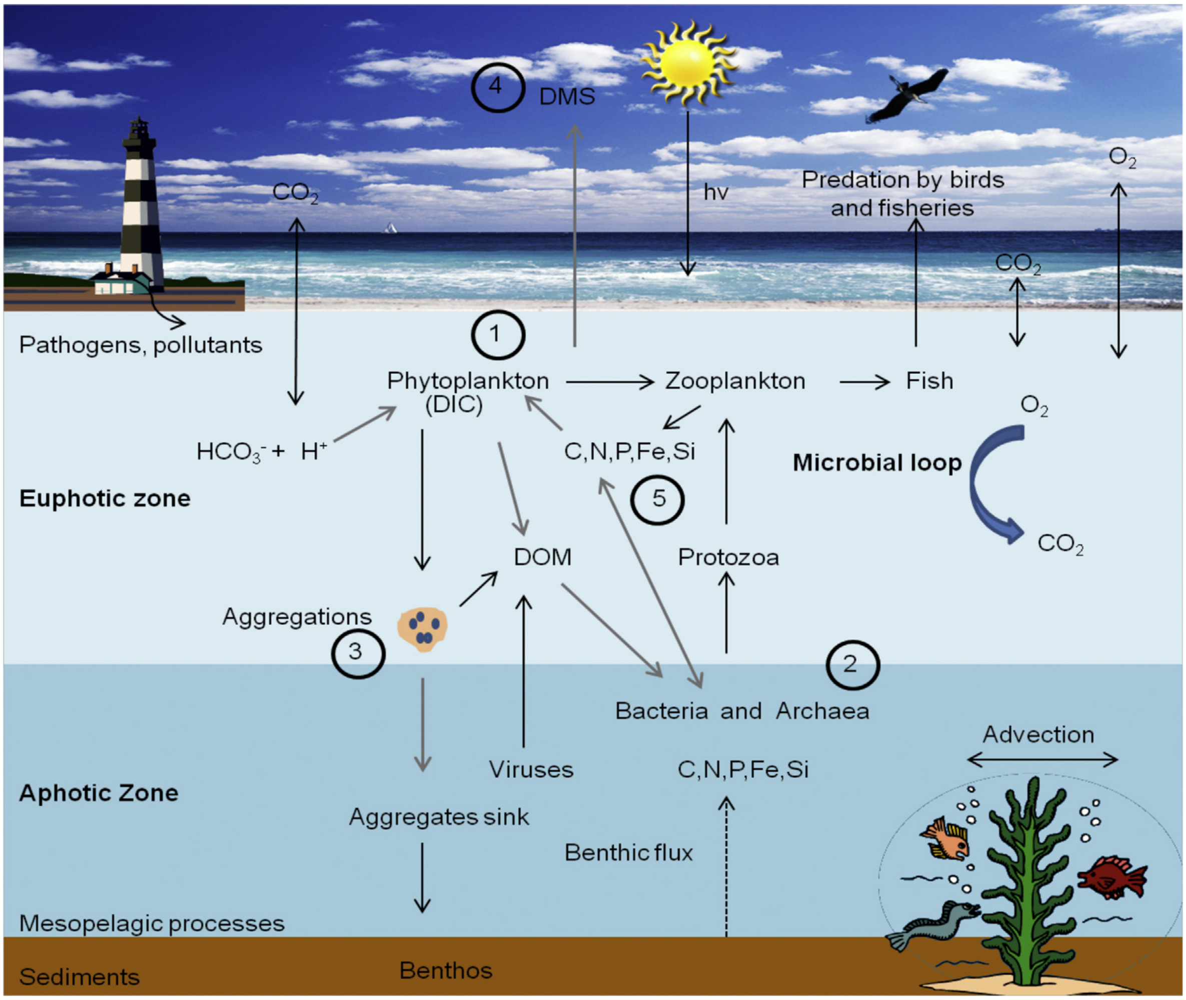

Figure 1 Key microbial processes in the marine environment susceptible to ocean acidification. Grey arrows and numbers indicate the processes that are likely to be affected by OA. (1) Primary productivity, (2) microbial composition and community structure, (3) microbial aggregation and interactions, (4) trace gases production, and (5) elemental cycles.

iron uptake process (Shi et al., 2010) due to the decrease in bioavailability of dissolved iron. Consequently, it affects the N_2 fixation as observed in case of *Trichodesmium* under iron-limiting conditions (Shi et al., 2012). The key reason behind decline in N_2 fixation is decreased photosynthesis under iron stress and subsequent decline in N_2 fixation. Thus, iron stress caused by OA indirectly affects the normal N_2 cycling in oceanic environments.

4.3. Trace gas emission

In marine waters, an ample mixture of trace gases (e.g. dimethyl sulphide, organohalogens, ammonia, nonmethane, oxygenated hydrocarbons, volatile oxygenated organics and nitrous oxide) are formed by various biological and photochemical processes (Archer et al., 2013; Liss, 2007). Most of the marine microbes are responsible for the emission of these trace gases that play a significant role in both marine and atmospheric processes (Beerling et al., 2007; Carpenter et al., 2012; Schimel and Gulledge, 1998).

Dimethyl sulphide (DMS), one of the crucial trace gases is generated from dimethyl sulfoniopropionate (DMSP). DMS helps in the formation of cloud condensation nuclei (CCN), and affects cloud cover over the ocean. Phytoplanktonic enzymatic DMSP lyase, heterotrophic bacteria and viral lysis are three major mediators for the conversion of DMSP to DMS. Eukaryotic marine phytoplankton synthesize DMSP (non volatile), which gets released to seawater most likely by viral lysis of phytoplankton (Yoch, 2002). The release of DMSP is then converted to volatile DMS either by heterotrophic marine bacteria or by indigenous DMS lyase produced by phytoplankton. DMS is one of the non-anthropogenic sulphur input to the atmosphere (Hill et al., 1998). OA has been shown to affect the availability of viruses, thus it has the ability to indirectly influence marine trace gas emission (Larsen et al., 2008). In an another study, Wingenter et al. (2007) observed a rise in DMS and chloroiodomethane (CH_2ClI) under elevated CO_2 conditions. However, an increase in CH_2ClI level could cause a feedback due to rise in global warming as CH_2ClI results in the destruction of ozone and aerosol nucleation.

Thus, a change in ocean water chemistry will have direct effect on trace gas emission from marine sources. Doubling of current atmospheric CO_2 will cause significant decline in trace gas emission. Any changes in the production rate and sea-to-air emission of marine trace gases because of OA could have large impacts on atmospheric chemistry and global climate (Hopkins et al., 2010).

4.4. Extracellular enzyme activity and degradation of organic matter

Huge diversity of marine microorganisms constitutes the imperative component of marine ecosystem, which are involved in decomposition, mineralization and recycling of organic matters. Marine microorganisms decompose the larger macromolecules into a compatible molecular size, which facilitates free diffusion inside the cell (Weiss et al., 1991; Yamada et al., 2012). The decomposition of polymers and organic compounds is mediated by cell bound or extracellular enzymes. In the marine environment, organic matter is chiefly composed of high molecular weight dissolved organic matter (DOM). Therefore, activity of heterotrophic bacteria is crucial for the flux of DOM in the ocean. Thus, microbes and their extracellular enzyme activity make organic nutrient available for themselves and other organisms (Cunha et al., 2010; Ruiz-González et al., 2013). Change in ocean water pH is principally observed in surface ocean water, as it is in direct contact with atmospheric exchange of gases (Raven, 2005). The heterotrophic bacteria at the surface ocean decompose 75—95% of the organic matter generated by autotrophic organisms (Boyd et al., 1999). Thus, the consequence of OA on microbial activity is also chiefly expected in surface ocean.

Enzymes are sensitive to pH changes as they exhibit specific activity in narrow pH range. Even small change in pH can decrease the enzymatic rate (Dutta et al., 2006; Mobley et al., 1984). Intracellular enzyme activity is protected from environmental changes by the cytoplasm buffering system. However, the activity of extracellular enzymes in aquatic environments has also been shown to be sensitive towards changing pH (Cunha et al., 2010). Microbial cellular processes, along with their extracellular enzyme activity can be significantly altered by OA. Grossart et al. (2006) found that the activity of bacterial protease, α-glucosidase and β-glucosidase was highest at elevated pCO_2 level. Similar findings were reported by Piontek et al. (2010) who found increased microbial polysaccharide degradation under acidification conditions. Yamada and Suzumura (2010) studied the effect of OA on extracellular enzymes and reported decreased activities of leucine aminopeptidase and lipase under simulated acidified conditions. However, protease and β-glucosidase activities did not show significant changes when the pH was decreased from 8.2 to 7.8. The expected consequence of increased extracellular enzymes activity under elevated pCO_2 is the increase of the availability of simple carbon sources. This may further stimulate the competition for inorganic nutrients and indirectly distress the primary production in the ocean (Volk and Hoffert, 1985).

4.5. Microbial diversity and composition

The ocean encases miscellaneous habitats in which a diverse group of microbes live, with several thousands of bacterial species in each litre of surface seawater (Das et al., 2006; Joint et al., 2009). However, the complete knowledge of seawater microbial community is limited. Most of the marine microbes come under the category of viable yet uncultivable groups and only a small fraction of marine microbes have been cultured successfully (Dash et al., 2013). This might be one of the reasons of less exploitation of marine microbes to be used as model organisms for OA or other climate changes. Investigation on the response of microbial diversity to changes in pCO_2 showed considerable impact (Liu et al., 2010). Most of the studies on the response of microbial diversity due to change in pCO_2 showed promising results (Ibrahim et al., 2014; Liu et al., 2010; Motegi et al., 2013; Raulf et al., 2015). However, the majority of studies showed that actually the change in pH affects biogeochemical cycling processes rather than diversity (Capone and Hutchins, 2013; Dore et al., 2009). Using a culture dependent microcosm approach, Krause et al. (2012) investigated and reported that even a small pH shift can have direct effect on bacterial community composition from the North Sea. They identified *Gammaproteobacteria*, *Flavobacteriaceae*, *Rhodobacteraceae* and *Campylobacteraceae* as phylogenetic groups responding remarkably to differences in pH. Reduced pH has also been shown to cause an increase in growth of many pathogenic microorganisms such as *Vibrionaceae* and *Alteromonadaceae* in corals (Meron et al., 2011). Moreover, responses by bacterial groups to pH vary with seasons and growth conditions (growth of pathogenic bacteria will increase in warmer ocean) (Karvonen et al., 2010). pH dependent changes in bacterial diversity and composition is largely contributed by *Flavobacteriaceae* in many studies (Krause et al., 2012; Witt et al., 2011).

Maas et al. (2013) studied the response of bacterial community in the Ross Sea, Antarctica towards OA using T-RFLP RNA profile. T-RFLP RNA covers only metabolically active fraction of bacteria. They concluded that the bacterial diversity varies with incubation period under acidified conditions. Thus, it is speculated that prolonged exposure to pH shifts will substantially modify microbial composition of the oceans. Moreover, the overall diversity of microbes is not just dependent on pH changes at individual level.

4.6. Impact on microbial biofilms

Biofilms are a multicellular sessile community of microbes in which cells are embedded in a matrix of extracellular polymeric substances (EPS) (Jain et al., 2013). In marine environments, submerged surfaces are often colonized by microbes resulting in the formation of a biofilm. Biofilms under natural environmental conditions are composed of millions of microbial cells (single or multiple species) as opposed to free-living cells (Mangwani et al., 2014a). Formation of biofilm is a multistep process, which starts with attachment of a planktonic cell to a surface, followed by cell division, synthesis of exopolymers, co-aggregation/autoaggregation of cells, maturation and dispersal (Mangwani et al., 2014b). The structural features and organization of biofilm is decided by the species composition of the biofilm. The common culturable bacteria studied for marine biofilm are *Exiguobacterium*, *Bacillus*, *Halotalea*, *Micrococcus*, *Halomonas*, *Arthrobacter*, *Jeotgalibacillus*, *Pseudoalteromonas*, *Pseudomonas*, *Paracoccus* and *Vibrio*, to cite a few (Dash et al., 2014; Inbakandan et al., 2010; Lee et al., 2003; Webster and Negri, 2006). The matrix component of biofilm is a composite organization of polymeric biomolecules rich in polysaccharides, proteins, nucleic acids and uronic acid. However, at high pCO_2 an increased uronic acid content in the EPS matrix by biofilms of an indigenous microbial population was observed by Lidbury et al. (2012).

Witt et al. (2011) reported changes in microbial species composition in natural biofilms from the Great Barrier Reef under elevated pCO_2 level. They observed a decrease in the relative abundance of *Alphaproteobacteria* and an increase in the relative abundance of *Flavobacteriales* at low pH. Microbial biofilms are supporting structures of the coastal ecosystem amalgamating organic matter, cycling nutrients and providing grazing for marine invertebrates (Lidbury et al., 2012). Any change in community structure of biofilms can influence the settlement of invertebrate larvae in some cases (Qian et al., 2007; Roberts et al., 1991; Totti et al., 2007). Marine bacterial biofilms can obstruct settlement of larvae in barnacle *Balanus variegatus* and *Balanus larvae* (Keough and Raimondi, 1995; Maki et al., 1988). Whereas, in bryozoans (e.g. *Bugula stolonifera* and *Bugula neritina*) and polychaete (e.g. *Hydroides elegans*), biofilms have positive effects on larvae settlement (Keough and Raimondi, 1995; Lau et al., 2002, 2005). Thus, biofilms in the marine environment incorporate both microorganisms and eukaryotes. As a result, changes in microbial diversity of the biofilms could also cause ecosystem alterations. Simulated mesocosm studies to elucidate the effect of future ocean pH shift on biofilms confirm changes in structure of heterotrophic planktonic free-living bacterial communities (Allgaier et al., 2008; Liu et al., 2010; Witt et al., 2011). The underlying reason behind community shift has not been documented adequately. However, it is speculated that changes in community structure may be due to increase in polysaccharide synthesis with simultaneous increase in the activity of extracellular enzymes in biofilm (Piontek et al., 2010). Thus, overall response of microbial biofilms under elevated pCO_2 environment may be used as biological markers for OA and rising CO_2 (Lidbury et al., 2012).

4.7. Quorum sensing

Quorum sensing (QS) is a population density dependent communication process in bacteria via signalling molecules known as autoinducers (AI). QS is regulated via autoinducing peptides (AIPs) and acyl homoserine lactones (AHLs) in Gram-positive and Gram-negative bacteria respectively. AHLs and autoinducer-2 (AI-2) have numerous functions at many levels of biological and ecological organization in the marine environment (Chong et al., 2012; Manefield and Whiteley, 2007). The representatives of AHL producing genera are abundant in the marine environment and most of them are in the group *Proteobacteria* (Manefield and Turner, 2002). In the marine environment, AHLs mediate interactions between different species of bacteria.

QS in marine bacteria regulates a large number of processes, such as bioluminescence, symbiosis, competence, virulence, secondary metabolites, extracellular enzymes and biofilm formation (De Kievit, 2009; Mangwani et al., 2012; Miller and Bassler, 2001; Weber et al., 2009). At the same time, various bacterial species make use of QS autoinducers to establish an association with higher organisms. AHLs producing numerous *Gammaproteobacteria* live in association with corals, biofilms, sponges, algae and animals in marine environments (Dobretsov et al., 2009). Thus, QS is one of the key phenomena that influences microbial interaction at each trophic level of marine ecosystem.

OA has been reported to play a role in shifting of microbial community from *Gammaproteobacteria* to *Flavobacteriaceae* (Krause et al., 2012) and it modulates the AHL regulated support offered by *Gammaproteobacteria*. Thus, OA can also modify the QS process in the ocean, which may have effects on higher organisms (such as corals, sponges, alga and vertebrates) living in proximity of these microbes. For example, in the alga *Ulva* sp., the presence of AHL positive bacteria (e.g. *Vibrio anguillarum*) stimulates spore settlement. Golberg et al. (2011) characterized microbes associated with corals and found that 30% of the beneficial microbes associated with corals have AHL mediated QS.

Corals associated microbial community produce both QS inducers (for interaction) and QS inhibitors (as a protection against pathogenic microbes) (Generous, 2014; Ransome et al., 2013). The decline in pH due to OA favours the growth of pathogenic microbes in the nearby corals. As a defence mechanism, corals and few coral associated microbes synthesize number of QS inhibitors to protect themselves from pathogenic microbes (Golberg et al., 2011; Skindersoe et al., 2008). Thus, OA is expected to increase the production of QS inhibitors (Meron et al., 2011; Tait et al., 2010). The decline in calcification process in corals will also affect a balance between QS inducers and inhibitors (Krediet et al., 2013; Sharp and Ritchie, 2012).

5. Experimental tools/approaches to investigate the effect of ocean acidification on marine microorganisms

The decrease in pH of the ocean is a very slow process and conducting experiments in simulated conditions at laboratories is also very difficult. The gradual acidification process in nature and in artificial conditions will act differently on the physiology of a living system. Although it is speculated that the ocean chemistry affects microbial diversity and functioning, adequate literature is not available to deduce a strong conclusion. Thus, a thorough investigation on the effect of OA on diversity and ecosystem is need of the hour. Advancement in technology such as the use of high-throughput DNA sequencing has revolutionized the experimental approaches of exploring microbial genome and community profiling. Additionally, other advanced techniques such as ecogenomics, flow cytometry and mesocosm studies can be implemented to study the effect of OA on marine microorganisms.

5.1. Microorganism as a model to study future changes in ocean carbonate chemistry

Marine microorganisms are major mediators, which regulate a variety of biochemical processes. Any changes in microbial composition and diversity can affect many key physiological and biochemical progressions (Weinbauer et al., 2011). The response of marine microbes towards OA is supported by fewer experimental data. However, the genomic flexibility of microbes make them ideal nominee to be used for studies of OA at genetic level. Both autotrophic and heterotrophic marine microbes can be of tremendous value in a field study of climate change models with respect to living systems (Liu et al., 2010). Impact of OA, using marine microbes as model can be studied using the null hypothesis that marine microbes are highly adapted to OA and no catastrophic change occurs on the marine microbes driven biogeochemical cycles in marine environment (Joint et al., 2011).

Additionally, the marine microbes can be a huge asset to study the OA phenomenon due to their huge diversity in terms of composition, ecosystem function as well as many other unique characteristics. The major unique features include their short generation time, involvement in major biogeochemical cycling, trace gas production and they are easy to isolate and culture in laboratory conditions. Thus, they can be used to investigate evolutionary process as well as to understand the relationship between biogeochemical cycling in relation to biology. Bacterioplankton (cyanobacteria) are major primary producer in the ocean, exporting massive amounts of carbon to ocean that robustly affects the ocean carbon chemistry. Rising ocean CO_2 and temperatures may modulate surface ocean stratification, which in turn will affect the surface-water light regime and nutrient input from deeper layers. Bacterioplankton will be affected by these environmental changes in many ways besides playing a central role in mitigating climate changes (Liu et al., 2010; Ruiz-González et al., 2013; Siu et al., 2014).

Manipulation in carbonate chemistry, its effect on photosynthesis and other nutrient cycles governed by microbes can be studied using microbes as a model (Tanaka et al., 2008). Moreover, OA considerably modify microbial diversity, community and enzymatic activities under elevated pCO_2 (Lidbury et al., 2012; Weinbauer et al., 2011). Thus, marine bacterioplankton can be affected by OA either directly due to chemical changes at low pH or indirectly through the response of other organisms. OA have direct effect on calcification and primary production. Whereas, processes such as N_2 fixation, QS, elemental cycle and trace gases production are indirectly associated with OA. Another important process vulnerable to OA is nitrification. Nitrification is the oxidation of ammonia into nitrite and further oxidation into nitrates. OA can significantly decline the global nitrification rate in ocean (Beman et al., 2011). These changes serve as critical parameters in the effect of OA on marine microbes and ecosystem. Additionally, due to the rapid growth rate, marine microorganisms are most suitable model to study impact of OA on a global scale within a short period.

5.2. 'Omic' approach: ecogenomics

Genomic tools to understand the mechanisms and the processes that are altered in marine organisms by OA are potentially important for the research community. Ecogenomics, ecology studies in combination with genomic and proteomic approaches, have also been used to study the response of marine microorganisms to OA (de Boer et al., 2007). For instance, Larsen et al. (2008) showed the abundance of EhV, the virus infecting *Emiliania huxleyi* at elevated pCO_2, i.e. 1050 μatm. Additionally, proteomics can be applied to study the proteins that are actively participating under changing carbonate chemistry. Functional genomic approaches that focus on the dynamic aspects such as gene transcription, translation, and protein—protein interactions are also useful to study the influence of OA on marine microorganisms (Gilbert et al., 2008). The key complexity to predict the effect of ocean water pH on microbes is to distinguish between acclimatization and adaptation. Transcriptomics, measurement of all mRNAs in a biological sample using microarrays has extensively been used in marine ecology by some researchers (Hofmann et al., 2008; Keeling et al., 2014; Ti, 2013). Transcriptomic studies have the potential to elucidate the pathways that are influenced by abiotic stress and are used to develop fast resources to assess the impact of OA (Gracey, 2007; Maas et al., 2013). Thus, ecogenomics, transcriptomics, proteomics and the assessment of the expression of specific marker genes for crucial functions can be regarded as a useful tool for predicting the consequence of OA (Dupont et al., 2010; Liu et al., 2010).

5.3. Mesocosm experiments

Since the marine environment is very much dynamic, mimicking this environment and predicting the microbial response is quite difficult (Koch, 2007; Sciandra et al., 2003). Thus, laboratory investigations on a small scale can provide useful information about the impact of climate change on marine organisms. Mesocosm studies can be conducted in field to provide a semi-natural environment to study the impact of climate change on marine organisms (Engel et al., 2005; Grossart et al., 2006; Riebesell et al., 2007). Mesocosms can vary from the large bodies of sea-water to a few hundred litres to dozens of cubic metres including all its organisms (Stewart et al., 2013).

6. Key problems associated with ocean acidification studies

Diverse group of microorganisms are the most suitable live models to study OA. However, most of the studies so far dealing with impact of OA on microorganisms are limited to mesocosms lasting for only a few days. For instance, Labare et al. (2010) monitored the effect of OA on *Vibrio* sp. over the period of 72 h and found morphological changes in cell membrane under elevated pCO_2. In an another short-term study, Beman et al. (2011) reported noteworthy decrease in ammonia oxidation under acidified conditions. These experiments may lead to ambiguity, as the microbes possess the credential to acclimatize in the changing environmental conditions, the response of which cannot be predicted using short-term mesocosm studies (Liu et al., 2010). Thus, to gather ample information regarding adaptation of marine microbes to OA, there is a need of long-term experiments in addition to the functional genomic level studies (Nielsen et al., 2010; Roy et al., 2013). Current understanding about marine microbial physiology is inadequate to sufficiently understand the consequences of OA (Keeling et al., 2010; Range et al., 2011). Basic studies on microbial physiology may require development of new techniques. Most of the feasible laboratory scale experiments deal with a single species, which is not the correct representative of microbes in the natural environment. Omic approaches, such as metagenomic and metatranscriptomics are helpful in accessing genomic information of natural populations. However, a significant portion of the sequence has no known function. Mesoscale CO_2 enrichment experiments are technically difficult due to the presence of unnatural CO_2 concentration over large surface area of the ocean. Extending mesocosm experiments to the open ocean is also technically very demanding and is logistically very difficult. Standardized techniques are not available to study physiological parameters. In another aspect, space and time dependence of experimental outcomes may give rise to contrasting results. For instance, experiments conducted in North Sea may give rise to interesting results compared to the ones in the Arctic. Similarly, coastal communities may respond differently from the offshore ones. Thus, a throughout investigation around the marine ecosystem of the globe is necessary for proper assessment of the effect of OA on marine ecosystem as well as their inhabitants.

7. Concluding remarks

There is a building awareness about OA and how it might impact the marine environment in the years to come. Diverse group of microorganisms are the first to respond to the environmental changes due to their unique propensity of large surface area to volume ratio and genomic complexity. They are the most integral part of the marine ecosystem due to their involvement in major biogeochemical cycles and trace gas production. Although numerous research initiatives have contributed to study ocean carbonate chemistry and the impact of OA on marine organisms and ecosystem, understanding its effect on marine microbes at functional genomics level is especially lacking. Therefore, several aspects at microbial physiology and genomics are still under-explored to tackle this environmental problem of ocean water and to predict the future ocean scenario in terms of biological productivity.

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