To: Biofouling

Mini Review

Title: The oceans are changing: impact of ocean warming and acidification on biofouling communities

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Abstract

Climate change (CC) is driving modification in the chemical and physical properties of estuaries and oceans with profound consequences for species and ecosystems. Numerous studies investigate its effect from species to ecosystem levels, however little is known on impacts on biofilm communities and bioactive molecules, like cues, glues, and enzymes. CC is induced by anthropogenic activity increasing greenhouse emissions leading to rises in air and water temperatures, ocean acidification, sea level rise and changes in ocean gyres and rainfall patterns. These environmental changes are resulting in alterations in marine communities and spreading of species (pathogens, invasives). This review provides insights and synthesis of knowledge about the effect of elevated temperature and ocean acidification on microfouling communities and bioactive molecules. The existing studies suggest that CC will impact production of bioactive compounds, growth and composition of biofouling communities. Undoubtedly, with CC fouling management will became an even greater challenge.

Keywords: Biofilm, Biofouling, Bioactive compounds, Climate change

1. **Introduction**

The carbon dioxide concentration in the Earth's atmosphere is clearly and steadily rising (IPCC 2013). Anthropogenic emission has driven CO_2 concentration in the atmosphere from 208 ppm during the pre-industrial era to well over 400 ppm at the Hawaii monitoring site since 2015 with an estimated increase of 2ppm per year (https://www.esrl.noaa.gov/gmd/ccgg/trends/weekly.html). This increase in CO_2 concentration in the atmosphere causes many physical consequences for marine environments including ocean warming (IPCC 2013). The mean global sea surface temperature is increasing at an average rate of >0.1˚C per decade (over the last 39 years), with the strongest warming trends found at high latitudes, and with future prediction estimating an increase of 2.7 ˚C by 2090. Temperature variations are often accompanied by changes in salinity due to reduced or enhanced precipitation relative to evaporation. Freshening and warming cause enhanced density stratification (IPCC 2013) and reduce the depth of winter mixing, which can cause a decrease in O_2 concentration in Oxygen Minimum Zones which are higher than the estimated decrease in O_2 concentration in the Open Ocean (mean rate in the of 0.1 to >0.3 µmol $Kg^{-1}yr^{-1}$) (IPCC 2013). Additionally, climate change is expected to increase upwelling frequency and intensity, lead to sea level rise due to melting of sea ice and glaciers (Doney et al. 2012).

Increase in the level of atmospheric CO_2 will lead to ocean acidification (Doney et al. 2009). Because the oceanic and atmospheric gas concentrations tend towards equilibrium,~ 30% of the atmospheric CO_2 has been taken up by the oceans, decreasing average pH by~ 0.1 pH_T unit and ultimately changing water chemistry. The observed decrease in pH_T corresponds to a 26% increase in hydrogen ion concentration of seawater (Feely et al.

2009). By 2100, pH is expected to change by -0.13 (421ppm under RCP2.6), -0.22 (538ppm under RCP4.5), -0.28 (670ppm under RCP6.0) and -00.42 pH_T unit (936ppm under RCP8.5). Some progress has been made to understand the consequences of changes in pH, carbonate CO_3^{2-}, and the saturation state of $CaCO_3$ for marine organisms and ecosystems (IPCC 2013; Wahl et al. 2015). These chemical and physical changes have direct implications for physiological processes such as photosynthesis, calcification, growth rates and internal pH regulation in a wide range of organisms (McCoy and Ragazzola 2014, Nannini et al. 2015, Evans et al. 2017, Fabricius et al. 2017, Okazaki et al. 2017) which will lead in a disruption of marine ecosystems and a reduction of biodiversity (Hoegh-Guldberg et al. 2007, Milazzo et al. 2014, Beaugrand et al. 2015).

All industrial installations in estuaries, bays, seas and oceans, such as vessels, platforms, buoys, quickly develop biofouling, a community composed of micro- and macro-fouling organisms (Clare et al. 1992). Micro-fouling usually presents as a dynamic microbial biofilm, which is composed of various species of bacteria, microalgae and protozoa incorporated in a muco-polysaccharide matrix (Dobretsov 2010; Malaeb et al. 2013; Salta et al. 2013). Macro-fouling communities are complex, with barnacles, bryozoa, mussels, polychaetes and macroalgae being the most common (Richmond & Seed 1991; Zardus et al. 2008). In some cases, micro-fouling organisms produce chemical cues that induce or inhibit settlement of macro-fouling species (Crisp 1984; Dobretsov et al. 2006; Hadfield 2011; Qian et al. 2007; Rittschof 2017) while in others there is a little direct relationship between macro- and micro-fouling.

Biofouling has a huge economic impact on maritime industries (Callow & Callow 2002; Trepos et al. 2014). Biofouling clogs aquaculture nets, water intakes, heat exchangers and reduces ship hull performance (Okamura et al. 2010; Schultz et al. 2011; Sievers et al. 2014). Moreover, biofouling increases corrosion, shear stress and drag, eventually leading to higher fuel consumption (Schultz et al. 2011) and increased production of CO_2 and carbon particulates.

There are numerous reports of the effect of single environmental factors associated with climate change (CO_2 level, elevated temperatures and acidification) on individual benthic species (Bamber 1990; Parker et al. 2011; Lane et al. 2013; Calosi et al. 2013; Peck et al. 2015). Some of these benthic species, like the blue mussel *Mytilus edulis*, are potent biofouling species. In contrast, the percent of biofouling publications dealing with climate change is quite low but increasing every year (Figure 1). Several publications report effects of factors associated with climate change on micro- and macro-fouling communities on inert substrates (Kim & Micheli 2013; Gladis-Schmacka et al. 2014; Peck et al. 2015) and living hosts (Nasrolahi et al. 2012; Stratil et al. 2013; Saderne & Wahl 2013; Saha et al. 2014).

A significant proportion of the biofouling-related climate change literature addresses invasive species (Stachowicz et al. 2002; Hellmann et al. 2008; Canning-Clode et al. 2011). Invasive species can be introduced by ship fouling and in ballast water (Davidson et al. 2008, 2009; Sorte et al. 2010; Keller et al. 2011). Most biofouling-related climate change literature deals with species (organismal level) or populations of individual species (Figure 2). Fewer researchers investigated potential impact of factors associated with climate change on multispecies communities. The lowest number of publications report effects of factors associated with climate change on signaling molecules and the biochemistry of organisms (Poloczanska & Butler 2009) (Figure 2). The impact of climate change on microbial communities and the bioactive molecules they generate is understudied.

This review focuses on the impacts of elevated temperature and ocean acidification, on biofouling communities. Particular focus is on the effect of factors associated with climate change on bioactive molecules of fouling organisms and growth and composition of microbial communities. Finally, we suggest areas for fruitful future investigation and the implication of climate change on the antifouling industry.

2. Climate change and bioactive molecules from fouling organisms

Biologically active molecules are produced by all phyla of marine organisms and play important roles in signaling, communication, allelopathy (Mayer et al. 2013) and organization of marine communities (Browne et al. 1998; Hay 2009; Rittschof 2017). Chemical cues from bacteria, diatoms and fungi induce or inhibit settlement of invertebrate larvae and algal spores (Wieczorek et al. 1996; Zardus et al. 2008; Dobretsov et al. 2013). When released in the marine environment, most of these biologically active molecules are bio-transformed or biodegraded by microbes (Uroz et al. 2005; Moree et al. 2012). There is a straightforward relationship between increase in temperature and the half-life of biologically active molecules (Singh et al. 2004). Similarly, there is a positive relationship between the concentration of heterotrophic bacteria and the half-life of signal molecules (Decho et al. 2010). Elevated water temperatures due to climate change will stimulate growth of microorganisms and enhance biodegradation of cues as well as enhance synthesis of antimicrobial compounds by marine fouling organisms (Table 1).

Marine bacteria coordinate virulence, competence, conjugation, production of antibiotics, motility, and biofilm formation by quorum sensing (QS) (Miller & Bassler 2001; Waters & Bassler 2005; Williams 2007). QS is based on the production, release and detection of chemical signal molecules called autoinducers. Increased concentrations of these signals due to high bacterial population density lead to an alteration in gene expression that regulates bacterial physiological activities (Decho et al. 2011). One of the most common and studied class of QS signal molecules is acyl homoserine lactone (AHL) (Waters & Bassler 2005). AHLs are unstable at >pH 7 (Yates et al. 2002). Studies assessing the stability of AHL against alkaline hydrolysis showed that AHLs having longer acyl chains (>12 carbons) are more resistant to breakdown than their shorter counterparts (Hmelo et al. 2011). In laboratory and field experiments, pH has a significant impact on the concentration of AHLs in microbial mats (Decho et al. 2009). In phototrophic microbial mats, short chain AHLs degrade quickly during the day, when the pH is > 8.2. During the night, when pH is 6.8 the concentrations of AHLs increases (Decho et al. 2009). When shorter-chain AHLs are degraded too rapidly, cellular communication may be disrupted. Acidification due to climate change will have a dramatic effect on concentrations of AHLs (Table 1). Since AHLs are important for biofilm structure and composition and settlement of some macro-fouling species (Dobretsov et al. 2009), it is possible that changes in production of QS compounds will alter densities and compositions of biofouling communities.

Enzymes are biological catalysts that accelerate the rate of specific biochemical reactions. Most enzymes are proteins and their structure is important for their activity. Increased temperature and changes in pH can lead to partial inhibition and in extreme cases to inactivation of enzymes (Iyer & Ananthanarayan 2008). However, in other cases such as the activity of trypsin-like enzymes (Rittschof, 2017) increased temperature and lowered pH are near the optimum for the enzymes and increase rates of reactions. When marine organisms are subjected to environmental change (Hochachka & Somero 2002), the three main mechanisms used to maintain physiological homeostasis are: 1) quantitative (changing the concentration of enzymes and/or reactants); 2) qualitative (using a protein variant); 3) modulation (modifying the protein environment to reduce the impact of environmental change) (Clarke 2003).

Research shows that temperature impacts the enzyme levels and physiology of barnacles (Wong et al. 2011). Water temperature and high anthropogenic pollution have a significant effect on concentrations of antioxidant enzymes, such as catalase, superoxide dismutase and NADH-DT diaphorase, in the barnacle *Balanus (=Amphibalanus) amphitrite* (Niyogi et al. 2001). Anthropogenic ocean acidification alters protein expression patterns in *B. amphitrite* (Wong et al. 2011) although past studies have not found effects on reproduction due to changes in pH (McDonald et al. 2009, Nardone et al., 2018). The impact of temperature and pH on adhesion of barnacles has been reported (Tedesco et al. 2017).

Similarly, enzymes responsible for calcification of sedentary polychaete tubes were affected by elevated concentrations of CO_2 (Chan et al. 2012; Lane et al. 2013). Past work indicates the aragonite-producing juveniles of *Hydroides elegans* at the level of acidification predicted for the years 2050-2300 will not be able to maintain integrity of their calcification products (Chan et al. 2012).

Acidification affects interactions between iron and 3,4-dihydroxyphenylalanine **(**DOPA) and thus weakens byssus attachment of *Mytilus trossulus* to non-calcified materials

(O'Donnell et al. 2013). Mussel byssus threads were weaker and less extensible when secreted under elevated pCO_2 (>1200 μatm), whereas shell and tissue growth were unaffected (O'Donnell et al. 2013). Byssal fiber performance was reduced by 40%, which suggest that mussels will be dislodged by forces lower than those which dislodge them under present conditions. Decreased mussel attachment strength due to low pH was also reported by Zhao et al. (2017) who showed with real time PCR that low pH altered the expression of genes encoding proximal thread matrix protein, precursor collagen proteins and mussel foot proteins. The expression of some genes was down regulated, while others were up regulated. In multi-species communities, the impact of ocean acidification on mussel biomolecules became less predictable. A recent mesocosm study suggested that dense populations of macrophytes, like *Fucus vesiculosus* and *Zostera marina*, may mitigate acidification impact on mussel (*Mytilus edulis*) calcification by raising mean pH of seawater (Wahl et al. 2017). In the future, factors associated with climate change can change activity of enzymes and other bioactive molecules and, thus, change physiology and behavior of fouling organisms, and, finally, lead to changes in biofouling communities.

3. Climate change and microbial communities

Stress factors associated with climate change affect the growth and productivity of microbes (Rajkumar et al. 2013) and production of bioactive compounds (Hasegawa et al. 2005; Yang et al. 2007). Temperature has a dramatic impact on microbial growth (Price & Sowers 2004). Elevated temperature accelerates the growth of mesophiles and slows the growth of psychrophiles and alters the interactions between bacteria and their hosts (White et al. 1991; Wahl et al. 2012). In a case of marine pathogens, elevated temperature increases growth, virulence and antimicrobial resistance (Kimes et al. 2012; Abdallah et al. 2014). For example, at 28^0 C the infection rate and attachment of the coral pathogen *Vibrio shiloi* increases, while at the lower temperatures (about 16^0 C) bacterial adhesion and growth in the tissues of the host coral *Oculina patagonica* is minimal and does not cause bleaching (Toren et al. 1998; Kushmaro et al. 2001). Virulence factors involved in motility, host degradation, secretion, antimicrobial resistance and transcriptional regulation are up-regulated in the pathogen *Vibrio coralliilyticus* at temperatures above 27^0 C (Kimes et al. 2012).

Factors associated with climate change (e.g. increase in temperature, frequency of El-Nino and La-Nina-like conditions) and anthropogenically induced eutrophication cause massive algal blooms of microorganisms (Paerl & Huisman 2009). Due to presence of algal toxins and elevated oxygen consumption these blooms result in massive benthic and fish kills (Richlen et al. 2010; Hallegraeff 2010) and create estuarine and ocean dead zones (Diaz & Rosenberg 2008). In early July 2008, high level of nutrients and surface temperatures triggered a very dramatic bloom of *Ulva* sp. occurred in the China Sea off Qingdao, China (Leliaert et al. 2009). Similarly, in January-February 2014 extremely high ocean temperatures on the Atlantic coast of Brazil stimulated the largest algal bloom in the country's history. The bloom was composed of several species with the red alga *Aglaothamnion uruguayense* being the most abundant (Martins et al. 2016). In 2008-2009 in the Persian Gulf, an algal bloom of the dinoflagellate *Margalefidinium* (*Cochlodinium*) *polycricoides* probably brought by ballast waters caused high mortality among benthic animals and fishes (Richlen et al. 2010) and dramatically decreased biomass of biofouling communities (Dobretsov 2015). These examples suggest that algal bloom conditions are becoming the norm for most populated coastal regions and their impact on benthic and fouling community ecosystems will intensify in the warming oceans.

Marine biofilms are communities composed of viruses, bacteria, microalgae and protozoa incorporated in an exopolymer matrix (Zobell & Allen 1935; Webb et al. 2003; Qian et al. 2007; Dobretsov 2010). Biofilms are dynamic and the composition of communities can be altered by changes in environmental conditions, such as temperature, salinity, pH, and nutrient availability (Qian et al. 2007; Salta et al. 2013). For example, the number of rainy days and temperature affected growth of phototrophic biofilms on roof tiles (Gladis-Schmacka et al. 2014). Researchers studied the effect of different temperatures (high, low and ambient) on formation of microbial biofilms and subsequent larval settlement in laboratory experiments (Lau et al. 2005; Whalan & Webster 2014). Increased water temperatures led to formation of different microbial communities and subsequently affected settlement of larvae. Compositions of microbial communities associated with the alga *Fucus vesiculosus* were different when these algae were exposed to different temperatures or light intensities (Saha et al. 2014). Changes in pH led to significant decreases in biofilm performance and diversity (Patil et al. 2011). Peck and co-authors (Peck et al. 2015) studied formation of biofouling communities under ambient (pH = 7.9) and acidified (pH = 7.7) conditions at a constant temperature (23^0C). After 100 days in acidified conditions, the proportion of sponges and ascidians is increased but numbers of the spirorbid *Neodexiospira pseudocorrugata* were reduced 5-fold. Changes in pH affected microfouling communities as well; the densities of the diatoms were lower in the low pH treatments compared to controls (Peck et al. 2015). Similarly, the microbial communities of corals, coralline algae and foraminifera were significantly different after the exposure to pH 7.9 (pCO_2 = 822 μatm) over 6 weeks (Webster et al. 2013). In contrast, elevated pCO_2 had no impact on the microbiome associated with rhodoliths (Cavalcanti et al. 2018). If one ventures beyond the host algal thresholds to climate change, positive host-microbiome interactions are disrupted. Increasing temperatures resulted in a 2-fold increase in relative abundance of epibiotic Rhodobacteraceae on the surface of *F.vesiculosus* (Stratil et al. 2013). Similarly, community diversity measured by evenness and richness was higher at ambient water temperatures than at elevated temperatures. Thus, climate change can shift the structure of biofilms on inert and natural substrata (Table 1).

Biofilms play an important role by inducing or suppressing settlement of spores and larvae of some macrofouling species (Dobretsov et al. 2006; Zardus et al. 2008; Hadfield 2011; Salta et al. 2013). Thus, changes in microbial communities due to climate change could alter the structure of macro-fouling communities. For example, in the laboratory microbial communities developed at 23ºC and 30ºC were different from ones at 16ºC (Lau et al. 2005). Larval response to these biofilms was also different; biofilms developed in the laboratory at 23ºC and 30ºC stimulated settlement of larvae of the barnacle *B. (=A.) amphitrite* and *B. trigonus* but had no effect on the polychaete larvae *Hydroides elegans* (Lau et al. 2005). Similarly, biofilms developed at elevated temperatures stimulated sponge larval settlement (Whalan & Webster 2014). Changes in the microbial community associated with crustose coralline algae reduced coral larval settlement under low pH (Webster et al. 2013). UV radiation reduces densities of bacteria in biofilms, which in turn decrease settlement of *Hydroides elegans* (Dobretsov et al. 2005). These examples show that temperature and pH associated with climate change directly affect composition and densities of microorganisms in biofilms and indirectly (through biofilm composition and cues) reduce or enhance larval settlement of macro-fouling species.

4. Conclusions and future research directions

Climate change and increased anthropogenic activity will have strong effects on micro- and macro-fouling communities (Figure 3; Table 1). Though there are some publications on impacts of temperature, pH and generation of bioactive molecules, cues and signals associated with climate change at the species level, there is far less information about the impact of these factors at the community and molecular levels (Figure 2). This review suggested that increased temperatures and ocean acidification can affect compound production, detection, turnover and, in turn, will have a dramatic effect on microbial and macro-fouling communities.

Reports of the impact of ocean acidification on biofouling communities and their bioactive compounds are contradictory, indicating that responses are community dependent. Acidification will impact aragonite and magnesium calcite producers, such as coralline algae, corals, mussels, barnacles and some bryozoans (Doney et al. 2012; Chan et al. 2012; Lane et al. 2013). Acidified conditions significantly change biofouling community composition by a decrease in calcified (tube worms) and an increase in soft-bodied organisms, like ascidians and sponges (Peck et al. 2015). In contrast, some biofouling species (like *Amphibalanus amphitrite* and *Alcyonidium hirsutum*), their larvae and proteins are not sensitive to predicted changes in pH (McDonald et al. 2009; Saderne & Wahl 2013; Nardone et al., 2018). Moreover, dense populations of macrolagae, like *F. vesiculosus*, may reduce adverse effect of acidification on calcified biofouling organisms

(Wahl et al. 2017). Thus, it is likely that ecological impacts of ocean acidification will be location, species and community specific (Ekstrom & Moser 2014; Ekstrom et al. 2015). Future studies will answer questions about biofouling communities facing ocean acidification.

With climate change fouling management is a challenge (Table 2; Dobretsov 2009). Climate change will affect rates of leaching and dissolution of toxic ions and hydrolysis of copolymers of antifouling coatings because these are temperature, pH and flow dependent (Yebra et al. 2004; Yebra et al. 2006). Because coating chemistry and release rates are temperature sensitive, meeting environmental regulations in regions, which experience extreme temperatures, will be challenging. Additionally, spreading of invasive species (Sorte et al. 2010) will provide new challenges for industry. Novel regulations that will require coating companies to address these issues and provide new environmentally safe products that are effective in managing fouling in a warming and changing world are urgently needed.

As the polar ice melts, fast and inexpensive polar shipping routes are becoming possible (Lasserre & Pelletier 2011). In the future goods will travel on ships through the Arctic to Europe and Asia. However, the potential impacts of these new routes with respect to introduced and invasive species and performance of antifouling coatings remains unclear (Bax et al. 2003; Ware et al. 2014, Table 2). Long term information on biofouling communities in Arctic and preventive measures are lacking (Zvyagintsev 2003). Several important questions arise: Which invasive species have a change to establish in warming Arctic waters? Will polar port biofouling communities develop that are comparable to those found in temperate and tropical regions? Will antifouling coatings designed for temperate waters be effective and environmentally benign in warming Arctic? All of these questions should be answered urgently.

To conclude, we are at the beginning of our understanding of impacts of factors associated with climate change on bioactive molecules. The few existing studies suggest that ocean warming and acidification will have dramatic consequences on biofouling communities and their bioactive compounds. Probably, this effect will be region, community and species specific, which should be priority of future studies.

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