

Impacts of climate change on reactive oxygen species in seawater

Haeum Lee

Abstract

Reactive oxygen species (ROS) are highly reactive oxygen-containing molecules produced by the mitochondria due to anaerobic respiration and although some amount of ROS is natural, excessive ROS can be cytotoxic. This paper focuses on the impacts of climate change—decreasing oxygen level in seawater along with lowering pH level—on hydrogen peroxide (H_2O_2), the most abundant and most produced ROS in the ocean, and superoxide (O_2^-), one of the most crucial ROS associated with oxidative stress on living organisms. Due to the increased volume of greenhouse gasses emitted into the atmosphere, the ocean body is absorbing rampant excess carbon dioxide (CO_2). As a result, the pH of the seawater is dropping, making the ocean water acidic; this phenomenon is widely known as ocean acidification, one of the most significant consequences of climate change. Adding on to this stressor, the world's ocean is experiencing hypoxia, also known as ocean deoxygenation, where the oxygen level is declining in oceanic waters due to various human disruptions, such as the burning of fossil fuels, reduction of natural forests, and increased livestock farming, which all warm the seawater ultimately. This review highlights the direct and indirect effects of such changing oxygen and pH levels on ROS production in the ocean, as well as the influence of excess ROS production on marine lives, including cellular damage, oxidative stress, and metabolic process disruption. The investigation demonstrates how even though global climate change can affect aquatic mitochondrial activities, the production of ROS, its details, and consequences are yet to be explored.

Keywords: reactive oxygen species, superoxide, hydrogen peroxide, pH level, oxygen level, climate change

1. Introduction

The climate change crisis has a fatal impact on every corner of the globe, especially the sea. Due to the abrupt rise in greenhouse gas emissions, seawater has been experiencing a myriad of stressors, including ocean acidification and deoxygenation. Naturally, the ocean absorbs a certain amount of CO_2 and releases breathable O_2 ; however, oceanic water has sponged an increased quantity of CO_2 in recent years. As early as the Industrial Revolution during the late 18th century, CO_2 levels in the Earth's atmosphere have continuously increased, reaching their highest level measured in the history of humanity in this current decade (EPA, 2022). The cause behind this air pollution is various industrial production processes, primarily the burning of fossil fuels, which leaves extra CO_2 to linger in the atmosphere. Subsequently, due to increased CO_2 accumulation in the ocean, the ocean pH is decreasing to an acidic state (EPA, 2022). Another environmental stressor on the sea body, ocean deoxygenation, is also driven by human-induced factors. Ocean deoxygenation is caused by the warming of the seawater because warmer temperatures of ocean water have a lower oxygen affinity (Limburg et al., 2020). As marine organisms depend heavily on their environment, these two ocean-harming phenomena must be regarded when considering mitigations of climate change.

Various studies have revealed that changing environments can influence the production of reactive oxygen species (ROS) in marine organisms (Keyer et al., 1995; Selivanov et al., 2008; Link, 1988; Sutherland et al., 2019; Morris et al., 2022). The results of these studies showed that the lower pH of the surroundings directly impacts the ROS formation underwater—specifically superoxide and hydrogen peroxide formation—and that low oxygen levels induce more ROS creation (Zhu et al., 2022). Environmental factors (e.g., climate change) contribute to changes in the production of ROS, which will affect marine life as ROS can lead to cell death and oxidative stress (Zhu et al., 2022). Despite this, the direct correlation between climate change and the changing production of ROS has not been researched in depth. This review will outline the hidden consequences of climate change on the respiration and metabolism of organisms deep down underwater. The overproduction of ROS in marine species can lead to internal cellular damage, and the prolonged period of ROS production due to human interference can cause cell death, affecting ocean life as a whole.

2. Climate Change's Impact on the Ocean Chemistry

2.1 Ocean Acidification and pH Change

Before the Industrial Revolution in the 18th to 19th century, the ocean pH was about 8.2; however, in recent years, the pH is around 8.1 (EPA, 2022). Although the difference may be perceived as minor, the continuance of the dropping rate will yield fatal consequences. Even before industrialization, the pH of the ocean surface had been gradually declining. Ocean surface pH in the year 1770 was approximately $\sim 0.11 \pm 0.03$ higher across all oceans than the surface ocean in 2000 (Jiang et al., 2019). This was accelerated by the newer industrial technologies. Under current situations, the pH of the surface ocean will decrease at a rate of 0.02 units per decade, which will gradually accelerate to 0.04 units per decade as the end of the century approaches. Hence, from 2000 to 2100, the global ocean pH will decrease by 0.33 ± 0.04 on average (Jiang et al., 2019). These increased ocean acidification rates are unfortunate; therefore, it is essential to, at minimum, prevent the acceleration of the reduction in pH before the humans start facing deteriorating health, harsher weather, and dying natural habitats due to the rapid acidification of the ocean (Falkenburg et al., 2020).

In addition to the impact ocean acidification has on ROS, there are other various direct consequences of the acidification on marine life. An acidic environment can lead to neurosensory impairment and altered blood CO₂ chemistry (Esbaugh, 2018). Further, to talk about cellular impact, high fluctuation in pH recorded to lessen the metabolic rates of coral reefs (Barrot et al., 2021). In the long term, ocean acidification will reduce biodiversity, alter ecosystem functioning, and ultimately impact humans by reducing food supply, which could lead to malnutrition and frequent food poisoning (Falkenburg et al., 2020). Although people are becoming more aware of ocean acidification, there is yet to be a definite solution to prevent the oceanic water from becoming more acidic.

2.2 Ocean Deoxygenation and Oxygen Level Change

As seawater temperatures rise and ocean stratification—separation of ocean's body into layers by density—increases, oxygen O₂ in the seawater decreases. This process is occurring at a rapid pace, and it is expected that the ocean will lose up to 7% of its dissolved O₂ over the

next century (Körtzinger, 2010). As greenhouse gasses raise the ocean's temperature, the physical properties of water are affected, resulting in ocean "hypoxia"—a state when the oxygen level is low to the point of impairment (Limburg et al., 2020). O_2 , a compound not easily dissolved in water, becomes harder to dissolve when the water is warmer (Limburg et al., 2020). As 97% of the Earth's habitable space, the sea is the centerpiece to protecting all life on Earth. Additionally, at least 50% of oxygen in the atmosphere is produced by the ocean (Regaudie-de-Gioux et al., 2014).

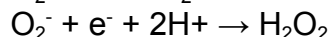
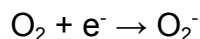
Low levels of dissolved oxygen pose several other direct threats to marine organisms. Lack of oxygen in the water can not only hinder growth, reproduction, and survival but also make organisms more likely to develop diseases (Limburg et al., 2020). Groups of animals less likely to utilize anaerobic respiration—the process of generating energy without oxygen—are susceptible to predation by other species more tolerant to hypoxia. As a result, the marine ecosystem will be significantly affected. Because nomadic organisms are likely to leave the low-oxygen areas, the ocean's ecosystem may undergo large migration, leaving other non-mobile organisms to perish (Limburg et al., 2020). As such, in the next couple of years, the ocean biodiversity may change drastically. To prevent this, climate change must be addressed seriously so that further deoxygenation of the ocean can be restrained.

3. Production of ROS in Marine Environments

All living cells produce ROS as a byproduct of anaerobic metabolism. Also known as reactive oxygen metabolites (ROMs), reactive oxygen intermediates (ROIs), and oxygen radicals, these oxygen-containing species, such as O_2^- and H_2O_2 , lead to oxidative stress when produced in excess (Li et al., 2016). However, in the ocean water, the exact causes of the production of extracellular ROS and its underlying mechanisms are yet to be researched thoroughly (Sutherland et al., 2019).

Although it depends on the change in Gibbs free energy between the reactants and the products (ΔG), ROS can interconvert. For example, as superoxide is highly unstable, H_2O_2 can be formed by superoxide dismutase (SOD)-catalyzed dismutation of O_2^- (Zorov et al., 2014; Fukai & Ushio-Fukai, 2011). Colored dissolved organic matter, found in all bodies of water, can absorb photons and enter an excited triplet state that can reduce O_2 to O_2^- , which can then go through dismutation to H_2O_2 (Equation 1; Morris et al., 2022).

Equation 1:



Hydrogen peroxide often has a longer lifetime than superoxide in the ocean; therefore, it is the main ROS used in the cell signaling of marine organisms (Morris et al., 2022). Instead, since superoxide is often produced with oxidative stress, it is the sign of marine life protecting themselves against invading pathogens (Morris et al., 2022).

4. Change in Production of Superoxide Due to Changing Environment

4.1 Production of Superoxide

Superoxide contains unpaired electrons, which makes it a free radical—a molecule capable of existence with one or more unpaired electrons; it is formed from the single-electron

reduction of molecular oxygen (Li et al., 2016). As a charged radical species, superoxide is toxic to marine organisms. Superoxides can easily react with extracellular proteins that lie on the surface or carbohydrates and inactivate their functions, which can be critical (Sudha et al., 2014). Carbohydrates in the ocean are crucial for bioactivities including antioxidative, antibacterial, and immunostimulatory (Fridovich, 1986; Sudha et al., 2014). Additionally, marine carbohydrates play a significant role in other biological processes such as pathogen recognition and cellular interactions (Vasconcelos & Pomin, 2018). These consequences come when superoxide becomes more prevalent in the ocean, and the rate of which it is increasing must be slowed down. In the seawater, the global rate of superoxide production is estimated to be about 3.9×10^{15} moles/year, which could change as a result of ocean acidification and deoxygenation (Sutherland et al., 2020).

4.2 Effect of pH Level Change on Superoxide Production

Superoxides in seawater exist chiefly in the deprotonated form, containing a resonance-stabilized form, and exhibit very minimum free radical character, making it relatively stable (Morris et al., 2022). However, when the pH of the oceanic water is altered due to ocean acidification, this stability may not be observed.

While various studies have investigated the consequences of ocean acidification, a notable lack of research exists on the direct impact of changing ocean pH on the production of superoxide in marine organisms (Jiang et al., 2019; Esbaugh, 2018). This gap in knowledge is concerning because superoxides serve as a reductant for iron, which, in turn, can stimulate the generation of hydroxyl radicals when transferring electrons to hydrogen peroxide. These hydroxyl radicals can cause DNA damage in different types of cells, underscoring the necessity for further investigation into this aspect of marine organism health (Keyer et al., 1995; Keyer & Imlay, 1996). Furthermore, when a cell contains high concentrations of superoxide, it may lead to oxidative stress and apoptosis, the classic death of cells (Buetler et al., 2004). When high levels of superoxide induce apoptosis, this may lead to various human health conditions such as ischemic damage, autoimmune disorders, and many different types of cancer (Elmore, 2007). Although the potential harms of apoptosis—caused by excess superoxide—on humans are well-known, research on its effect on life under the ocean is still largely unexplored. However, several of the marine organisms are known to be biologically similar to humans. Thus, it can be safely assumed that apoptosis will have similar effects on marine mammals and that it should be considered as one of the multiple harms that climate change is inflicting on the ocean. Considering the damage the overproduction of superoxide could have on marine life, it is important to be aware of how the ocean acidification crisis can directly influence the cell death of marine organisms, affecting biodiversity, the food chain, and the world's ecosystem as a whole.

4.3 Effect of Oxygen Level Change on Superoxide Production

Because superoxide is formed through the reduction of O_2 , producing more superoxide requires using more available oxygen in the ocean. It could be argued that—since superoxide comes from oxygen—less oxygen concentration will halt the production of superoxide. It may seem logical that more oxygen leads to more superoxide, and less oxygen would mean less of this harmful ROS. However, it is important to note that superoxide is the byproduct of a cell's anaerobic respiration. Therefore, with decreasing oxygen supply in the ocean, it can be

hypothesized that the production of superoxide will increase as more organisms will utilize anaerobic respiration in more frequent intervals. When monocytes were exposed to a very low O_2 concentration of 3%, they produced superoxide increasingly more (Palacios-Callender et al., 2004). Although more superoxide can indeed be produced with more available O_2 in a lab setting, in the ocean, it is the anaerobic respiration that results in the mass creation of superoxide (Palacios-Callender et al., 2004).

Additionally, as 3.9×10^{15} moles of superoxide are produced per year across all seas, 36% of the oxygen in the water is used up by superoxide production (Sutherland et al., 2020). The problem aggravates each year as less oxygen would mean more anaerobic respiration, ultimately resulting in even more production of superoxide—and the consequence of this is unexplored. Although it is clear that oxygen level directly impacts the increased production of superoxide, there are limited studies on the topic. The rate at which the production of ocean superoxide is changing, the consequences of increased superoxide production in the long term, and potential mitigation methods remain unknown. Also, the connection between climate change and superoxide is hardly discussed.

5. Change in Production of Hydrogen Peroxide Due to Changing Environment

H_2O_2 exists without any unpaired electrons, and therefore, it is not a free radical (Li et al., 2016). The presence of H_2O_2 affects water quality because it actively participates in metal redox reactions and causes oxidative stress for marine organisms (Zhu et al., 2022). Additionally, high concentrations of hydrogen peroxide can damage and kill phytoplankton, the food for countless marine animals.

5.1 Effect of pH Change on Hydrogen Peroxide Production

The environment growing more acidic has a substantial impact on the natural production of H_2O_2 . A study by Selivanov et al. (2008) demonstrated that, under the condition of an incubation medium without permanent anions, the rate of H_2O_2 release was at its lowest when pH was at 8.0. As the pH lowered below 8.0, there was a significant increase in H_2O_2 release, with its peak at pH 7.0, and from pH levels 7.0 to 6.0, the H_2O_2 production gradually decreased, but still being about 650 H_2O_2 pmoles/min/mg higher than when the pH was at 8.0 (Selivanov et al., 2008). Additionally, as pH lowers, H_2O_2 concentration gradually increases: nearly 0% when pH is 7.0, about 0.025% when pH is 6.0, and about 0.23% when pH reaches 3.0 (Wolanov et al., 2013). The trend in increasing H_2O_2 concentration in response to acidification illustrates that as the ocean's pH decreases, excess H_2O_2 will remain in the ocean body. To amplify that idea, the change in pH is associated with how the epithelial cells incubated with H_2O_2 survive. When pH was at 7.0, the survival rate of H_2O_2 -incubated cells was 9×10^{-2} . However, as pH dropped to 6.5, the survival steeply dropped to 1×10^{-2} , one-ninth of the rate when pH was 0.5 higher (Link, 1988). This finding distinctly shows that cells in low pH, with higher concentrations of H_2O_2 , are more prone to death compared to cells in high pH, with lower concentrations of H_2O_2 . Therefore, in a bigger scope, ocean acidification can induce the deaths of marine organisms, affecting the biodiversity and ecosystems of the ocean, and ultimately, of the world. Additionally, it is worth noting that the aforementioned research on the survival of cells with H_2O_2 was conducted *in vitro*. It is still vague what consequence this excess H_2O_2 will have in the vast ocean, and it

requires more attention because a thorough understanding of the effect is necessary to mitigate the issue.

5.2 Effect of Oxygen Level Change on Hydrogen Peroxide Production

Since both hydrogen peroxide and superoxide are ROS produced in the presence of oxygen, the impact of deoxygenation on hydrogen peroxide is similar to that of superoxide. The oxygen consumption of mammals is 31% higher in high-oxygen settings than in low-oxygen environments, and marine mammals are no exception (Munns et al., 2005). As climate change reduces dissolved oxygen from the ocean, marine animals have to survive with limited oxygen intake, leading to increased anaerobic respiration to produce adenosine triphosphate (ATP) and hydrogen peroxide from the mitochondria. Hydrogen peroxide is formed in eukaryotic cells as a result of oxygen hypoxia (Vergara et al., 2012). Thus, as a result of ocean hypoxia, it is highly likely that marine animals' mitochondria will participate in increased hydrogen peroxide production. Since ROS is produced in a deficit of oxygen by living organisms, such a hypoxia environment can induce extra generation of this ROS. Consequently, changes in the rate of hydrogen peroxide production might cause mitochondrial protons to leak, potentially affecting the use of cellular ATP involved in energy wastage and intracellular calcium turnover (Munns et al., 2005).

6. Recent Findings: Impacts of Microplastic on ROS Production

Recent studies have revealed the involvement of marine ROS in microplastics, which are growing abundant in the ocean (Das, 2023; Zhu et al., 2020). Microplastics, tiny pieces of plastic debris, can be deadly toxic to marine life. These small chunks of plastic can accumulate in the mitochondria of ocean organisms, disrupting the mitochondrial electron transport chain (Das, 2023). Consequently, this will lead to the production and different types of ROS, which are capable of damaging DNA and inducing other harmful consequences (Das, 2023). Considering this component, the ROS in the ocean body may be increasing more rapidly than expected due to large amounts of plastic being disposed of each day. Furthermore, research by Zhu et al. (2020) showed that there is a significant gap in research regarding the mechanisms of ROS production when microplastics are present in the ocean. Revisiting the consequences that ROS overproduction might have on the ocean and the world, the impact of microplastic on ROS is something that requires more attention and research, especially because large masses of plastic are trashed into the ocean each day. Aside from the well-known damage of plastic in the ocean—the consumption of plastics by ocean animals—the accumulation of microplastic in their mitochondria is a new scope in research, and by recognizing this phenomenon more, humans can address different oceanic consequences separately in a more oriented way.

7. Conclusion

In the era of climate crisis, a healthy image of the future environment is often difficult to envision. The inevitable consequence of industrialization brought Earth a deadly disease with the cure still in search. As fossil fuels continue to burn and greenhouse gasses continue to fill the atmosphere, a climate change crisis arises. It brings countless hazards to the ocean such as ocean acidification and deoxygenation.



As ocean acidification brings down the pH level of the ocean to a more acidic level, it is expected that ocean life will be affected by it. ROS are affected by this acidifying state of the ocean water (Buetler et al., 2004). Superoxide is directly affected by the acidic environment, where lower acidity stimulates the production of this ROS. Superoxide is already known to cause cell DNA damage (Keyer et al., 1995; Keyer & Imlay, 1996). Similarly with hydrogen peroxide, which can also be formed from superoxide, the more acidic the environment is, the more likely the hydrogen peroxide creation would increase dramatically (Wolanov et al., 2013; Link, 1988). With known information that pH can lead to overproduction of superoxide and hydrogen peroxide, the connection between the global climate crisis and marine animal cell death is still not widely addressed nor researched in depth. It is rarely mentioned that ocean acidification has the potential to release more of these ROS without control into the ocean body, and the impacts this would have not just on the marine animals but also on the world ecosystem and food network are also understated.

Although there are no current policies that directly address the problem of ROS overproduction, there still exist various laws and policies attempting to mitigate climate change and its effect on the ocean. To fight greenhouse gas emissions, the United States Environmental Protection Agency (EPA) passed the Clean Air Act to effectively reduce harmful emissions (Cropper et al., 2023; EPA Clean Air Act, 1970). Recently, the EPA further enforced the Clean Air Act by presenting more guidelines for CO₂ exclusively. To solve ROS overproduction, more data must be at hand. Thus, it is necessary to research deeper into the effects and consequences of long-term environmental changes that affect ROS production. Moreover, eliminating the root of the problem—low pH and oxygen in the ocean body—is also significant in addressing this issue. Kelp, as a natural absorbent of carbon and producer of oxygen, is the ocean's buffer to both ocean acidification and deoxygenation (Young et al., 2022). Therefore, preserving and fostering the ocean's kelp forests can be a solution to mitigate such ocean phenomena at once. However, such efforts may be futile when masses of greenhouse gasses are produced each minute and bulks of plastic are trashed in the ocean. With the fate of the planet in the hands of its inhabitants, global and holistic efforts must be made to save the planet.

References

1. Barott, K. L., Huffmyer, A. S., Davidson, J. M., Lenz, E. A., Matsuda, S. B., Hancock, J. R., Innis, T., Drury, C., Putnam, H. M., & Gates, R. D. (2021). Coral bleaching response is unaltered following acclimatization to reefs with distinct environmental conditions. *Proceedings of the National Academy of Sciences*, 118(22). <https://doi.org/10.1073/pnas.2025435118>
2. Buetler, T. M., Krauskopf, A., & Ruegg, U. T. (2004). Role of superoxide as a signaling molecule. In *News in Physiological Sciences* (Vol. 19, Issue 3). <https://doi.org/10.1152/nips.01514.2003>
3. Cropper, M., Muller, N., Park, Y., & Perez-Zetune, V. (2023). The impact of the clean air act on particulate matter in the 1970s. *Journal of Environmental Economics and Management*, 121, 102867.
4. Das, A. (2023). The emerging role of microplastics in systemic toxicity: Involvement of reactive oxygen species (ROS). *Science of The Total Environment*, 895. <https://doi.org/10.1016/j.scitotenv.2023.165076>
5. Elmore, S. (2007). Apoptosis: A Review of Programmed Cell Death. In *Toxicologic Pathology* (Vol. 35, Issue 4). <https://doi.org/10.1080/01926230701320337>
6. EPA. (2020). *Understanding the Science of Ocean and Coastal Acidification | Ocean and Coastal Acidification | US EPA*. United States Environmental Protection Agency (EPA).
7. Esbaugh, A. J. (2018). Physiological implications of ocean acidification for marine fish: emerging patterns and new insights. In *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* (Vol. 188, Issue 1). <https://doi.org/10.1007/s00360-017-1105-6>
8. Falkenberg, L. J., Bellerby, R. G. J., Connell, S. D., Fleming, L. E., Maycock, B., Russell, B. D., Sullivan, F. J., & Dupont, S. (2020). Ocean acidification and human health. *International Journal of Environmental Research and Public Health*, 17(12), 4563. <https://doi.org/10.3390/ijerph17124563>
9. Fridovich, I. (1986). Biological effects of the superoxide radical. *Archives of Biochemistry and Biophysics*, 247(1). [https://doi.org/10.1016/0003-9861\(86\)90526-6](https://doi.org/10.1016/0003-9861(86)90526-6)
10. Fukai, T., & Ushio-Fukai, M. (2011). Superoxide dismutases: Role in redox signaling, vascular function, and diseases. In *Antioxidants and Redox Signaling* (Vol. 15, Issue 6). <https://doi.org/10.1089/ars.2011.3999>
11. Jiang, L. Q., Carter, B. R., Feely, R. A., Lauvset, S. K., & Olsen, A. (2019). Surface ocean pH and buffer capacity: past, present and future. *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-019-55039-4>
12. Keeling, R. F., & Körtzinger, A. (2010). Ocean Deoxygenation in a Warming World - Annual Review of Marine Science, 2(1):199. *Annual Review of Marine ...*
13. Keyer, K., Gort, A. S., & Imlay, J. A. (1995). Superoxide and the production of oxidative DNA damage. *Journal of Bacteriology*, 177(23). <https://doi.org/10.1128/jb.177.23.6782-6790.1995>
14. Keyer, K., & Imlay, J. A. (1996). Superoxide accelerates DNA damage by elevating free-iron levels. *Proceedings of the National Academy of Sciences of the United States of America*, 93(24). <https://doi.org/10.1073/pnas.93.24.13635>
15. Li, Y. R., Trush, M., & Jia, Z. (2016). Defining ROS in Biology and Medicine. *Reactive Oxygen Species*, 1(1). <https://doi.org/10.20455/ros.2016.803>

16. Limburg, K. E., Breitburg, D., Swaney, D. P., & Jacinto, G. (2020). Ocean Deoxygenation: A Primer. In *One Earth* (Vol. 2, Issue 1). <https://doi.org/10.1016/j.oneear.2020.01.001>
17. Link, E. M. (1988). The mechanism of pH-dependent hydrogen peroxide cytotoxicity in vitro. *Archives of Biochemistry and Biophysics*, 265(2). [https://doi.org/10.1016/0003-9861\(88\)90139-7](https://doi.org/10.1016/0003-9861(88)90139-7)
18. Morris, J. J., Rose, A. L., & Lu, Z. (2022). Reactive oxygen species in the world ocean and their impacts on marine ecosystems. *Redox Biology*, 52. <https://doi.org/10.1016/j.redox.2022.102285>
19. Munns, S. E., Lui, J. K. C., & Arthur, P. G. (2005). Mitochondrial hydrogen peroxide production alters oxygen consumption in an oxygen-concentration-dependent manner. *Free Radical Biology and Medicine*, 38(12). <https://doi.org/10.1016/j.freeradbiomed.2005.02.028>
20. Palacios-Callender, M., Quintero, M., Hollis, V. S., Springe, R. J., & Moncada, S. (2004). Endogenous NO regulates superoxide production at low oxygen concentrations by modifying the redox state of cytochrome c oxidase. *Proceedings of the National Academy of Sciences of the United States of America*, 101(20). <https://doi.org/10.1073/pnas.0401723101>
21. Regaudie-de-Gioux, A., Lasternas, S., Agustí, S., & Duarte, C. M. (2014). How much oxygen comes from the ocean? *Frontiers in Marine Science*, 1(JUL).
22. Selivanov, V. A., Zeak, J. A., Roca, J., Cascante, M., Trucco, M., & Votyakova, T. V. (2008). The role of external and matrix pH in mitochondrial reactive oxygen species generation. *Journal of Biological Chemistry*, 283(43). <https://doi.org/10.1074/jbc.M801019200>
23. Sudha, P. N., Aisvarya, S., Nithya, R., & Vijayalakshmi, K. (2014). Industrial applications of marine carbohydrates. In *Advances in Food and Nutrition Research* (Vol. 73). <https://doi.org/10.1016/B978-0-12-800268-1.00008-1>
24. Sutherland, K. M., Coe, A., Gast, R. J., Plummer, S., Suffridge, C. P., Diaz, J. M., Bowman, J. S., Wankel, S. D., & Hansel, C. M. (2019). Extracellular superoxide production by key microbes in the global ocean. *Limnology and Oceanography*, 64(6). <https://doi.org/10.1002/lno.11247>
25. Vasconcelos, A. A., & Pomin, V. H. (2018). Marine carbohydrate-based compounds with medicinal properties. In *Marine Drugs* (Vol. 16, Issue 7). <https://doi.org/10.3390/md16070233>
26. Vergara, R., Parada, F., Rubio, S., & Pérez, F. J. (2012). Hypoxia induces H₂O₂ production and activates antioxidant defence system in grapevine buds through mediation of H₂O₂ and ethylene. *Journal of Experimental Botany*, 63(11). <https://doi.org/10.1093/jxb/ers094>
27. Wolanov, Y., Prikhodchenko, P. V., Medvedev, A. G., Pedahzur, R., & Lev, O. (2013). Zinc dioxide nanoparticulates: A hydrogen peroxide source at moderate pH. *Environmental Science and Technology*, 47(15). <https://doi.org/10.1021/es4020629>
28. Young, C. S., Sylvers, L. H., Tomasetti, S. J., Lundstrom, A., Schenone, C., Doall, M. H., & Gobler, C. J. (2022). Kelp (*saccharina latissima*) mitigates coastal ocean acidification and increases the growth of North Atlantic bivalves in lab experiments and on an oyster farm. *Frontiers in Marine Science*, 9. <https://doi.org/10.3389/fmars.2022.881254>



29. Zhu, Y., Powers, L. C., Kieber, D. J., & Miller, W. L. (2022). Depth-resolved photochemical production of hydrogen peroxide in the global ocean using remotely sensed ocean color. *Frontiers in Remote Sensing*, 3. <https://doi.org/10.3389/frsen.2022.1009398>
30. Zorov, D. B., Juhaszova, M., & Sollott, S. J. (2014). Mitochondrial reactive oxygen species (ROS) and ROS-induced ROS release. In *Physiological Reviews* (Vol. 94, Issue 3). <https://doi.org/10.1152/physrev.00026.2013>