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Algal Communities: An Answer to Global Climate Change

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Human activities and resultant changes in global climate have profound consequences for ecosystems and economic and social systems, including those that are dependent upon marine systems. The increasing concentration of atmospheric greenhouse gases (GHGs) has resulted in gradual modification of multiple aspects of marine ecosystem properties such as salinity, temperature, and pH. It is well known that temporal and spatial variations in environmental properties determine the composition and abundance of different algal populations in a region. Within the present study the evidence for algal compatibility to changing environmental conditions is surveyed. The unique ability of algal communities to play a role in promotion of CO₂ sequestration technologies, biorefinery approaches, as well as transition to CO₂-neutral renewable energy has gained traction with environmentalists and economists in a view to mitigation of climate change using algae. The next step is to re-evaluate the assumption of a steady-state oceanic carbon cycle and the role of biological activities in response to future climate changes.

(3.9%)^[1] will be accompanied by a 50% increase in fuel consumption.^[2] Economic growth based on fossil fuel will not only speed up CO₂ emissions and increase the consequences of climate change, but also eventually induce fuel security problems and rising energy prices which could impose negative economic effects on developing countries.^[3] Based on this model, prevention of climate change and the enhancement of energy security unite environmentalists and economists in reduction of fossil fuel combustion and CO₂ emissions as well as supporting a transition to CO₂-neutral renewable energy and promotion of CO₂ sequestration technologies.

Greenhouse gases (GHGs), as the main global air pollutants, have long-term damaging effects on climate. Atmospheric accumulations of CO₂ and other GHGs impose significant effects on global temperature;

human-induced greenhouse effects during the 20th century caused a global average temperature rise of about 0.7 °C^[4] and the Intergovernmental Panel on Climate Change (IPCC) has predicted a global average temperature increase of 1–6 °C by 2100.

Global warming is viewed as a public issue, requiring cooperative action to prevent serious environmental consequences. In working to achieve a higher level of collaboration among biologists and climate scientists, marine systems should be assessed to fully identify potentials to meet the global tension of climate change. Oceans can potentially adsorb huge amount of carbon through biological and non-biological processes. The absorption of CO₂ and a consequent significant reduction in the level of carbon in the atmosphere could mitigate or postpone global warming and avoid dangerous climate change.^[5]

Recent anthropogenic activities negatively affect environmental conditions and biota in the hydrosphere. What is currently known about the environmental consequences of climate changes in marine systems is summarized in **Figure 1**. Since these changing environmental properties may be related to or be caused by global climate change, the possible influences of climate change on the marine environments are illustrated with this Figure 1. In brief, the accumulation of the most important GHGs; water vapor (H₂O), carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O), and ozone in the atmosphere changes the energy influx and emission by

1. Introduction

Global human population growth amounts to 1.1% per year and it is estimated that the world population will take numbers to more than nine billion people by 2050. An insatiable appetite for energy, food, and also continued global economic growth

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ocean, so the algae growing in the oceans play a big role in moderation of the atmospheric CO₂ concentration.^[14]

2.1. Algae as Climate Change Indicators

Assessment of the dominant algae species in an ecosystem is an important potential strategy to survey the consequences of climate changes occurring in a region. Algal communities dynamically develop appropriate responses against different environmental variations such as rising temperature, changes in CO₂ concentration, osmotic stresses, and changes in pH.^[15,16] Evaluation of the relationship between changing environmental conditions in an ecosystem and changes in the characteristics of the algae populations has been recently introduced as bioindicator for the assessment of climate changes.^[17]

Phytoplankton communities could play a role as good indicators of climate change since: 1) they have no direct commercial exploitation, so populations are not perturbed by harvesting; 2) phytoplankton have short live cycles and their population size is less influenced by the persistence of individuals from previous years; and 3) they are free floating. These attributes together mean any long-term and/or rapid changes in the frequency, community dynamics, and presence of species in populations can be attributed to climate-induced changes at different levels of the ecosystems.^[18]

Monitoring of changes in biomass due to nutrient enrichment, changes in the rate of algae growth, changes in photosynthetic capacity, as well as studies of changes in water color due to algal blooms are frequently used as biological indicators during the study of the effects of climate change on algal communities. Physiological features, reproduction properties, and also the productivity of algae populations could be influenced by these changes. Accumulation of metal chelators, biosynthesis of stress proteins, or heat shock proteins (HSPs), development of defense mechanisms against oxidative stress as well as stimulation of detoxification pathways all have been introduced as metabolic responses that have potential as algal bioindicators to aquatic xenobiotic pollution.^[19]

A comprehensive knowledge of morphological and physiological features, habitat requirements, mechanisms of response to stressors (sensitivity, specificity, timescale), and ecological relevance is a key prerequisite of using algae cells as indicators. Scientists have used sediments and fossilized remains of algae in past studies.^[20] In a study by Desrosiers et al.^[21] it was found that diatoms are very suitable as bioindicators especially in high-latitude regions. The occurrence of different species of diatoms can be used to predict changes in water pH, changes in nutrients, changes in salinity, etc., because these changes can affect the size, shape, and structure of the silica cell walls of diatoms.^[21] These silica compounds can be precipitated in the deep ocean, lakes, and wetlands and can be used to study past environmental changes in the ecosystem in what is termed micropaleontology.^[22] Inter alia, micropaleontologists can shed light on past climate changes across geological time frames by studying the oldest fossils on Earth, stromatolites. Stromatolites are the remains of ancient cyanobacteria, or blue-green algae. There is evidence that they were first growing in shallow oceans when the Earth was still cooling^[23] and nowadays can be used as

a bioindicator to show environmental tension at different times. Other algae that are used as indicators for the assessment of climate changes are the Chrysophyceae and Synurophyceae.^[24] These two classes also contain remnants of silica.^[25] Some algae such as the Chlorophyta,^[26] cyanobacteria,^[27] and the Pyrrophyta^[28] do not contain silica and scientists study other morphological features, such as the capacity for forming colonies, and filaments formation. Pigment type and content, cell volume and size, species diversity, and storage nutrients in cells are frequently used as biomarkers for the presence of particular algal groups. These features can also be used to evaluate seawater quality and water pollution. For example, studying the growth and productivity of the macroalgae *Ascophyllum nodosum*, is suited to monitor the global warming effects at West Greenland and North Norway.^[29] In a different study, it was found that another brown alga, *Padina pavonica*, can be used as bioindicator to assess ocean acidification since *P. pavonica* is a sensitive reporter of acute environmental pH changes; acidified conditions induce decalcification and the uncovered *P. pavonica* is subject to the dangers posed by exposure to high light.^[30]

Algae can respond to changing environmental conditions. Tracking these responses can be regarded as quantitative bioindicators. These responses can be classified in two types: 1) Short-term responses which are expressed at the physiological and biochemical level and last for a few seconds to a few days (biomarkers) and 2) Long-term responses, for example, growth of various species in the environment and their success in competition.^[31] These responses last from several weeks to several years (bioindicators). Some ecological consequences of climate change impose physico-chemical variations in algal habitats. For example, ultraviolet (UV) radiation might impose negative effects on DNA synthesis, photosynthesis, biochemical features, biomass, and growth rate.^[32] Filamentous green algae, along with a wide range of other algal taxa, can protect themselves from the negative effects of oxidative stress caused by UV radiation because they have photoprotection mechanisms including phenolic compounds, carotenoids, and mycosporine-like amino acids.^[32] Measurement of the afore-mentioned compounds or other biochemical and physiological characteristics can be used as biomarkers for stress when the result can be compared to control populations.^[33]

Other features that can be used as biomarkers include the capacity of algal cells to respond to trace metal ions. Regarding to the mechanism of accumulation of trace metals in algal cells, measurement of the related responses (e.g., accumulation of chelating agents, ascorbate, and glutathione) could also be used as biomarkers.^[34] It should be noted that the production of these compounds might also be stimulated by other environmental tensions (e.g., UV radiation) that cause stress to the algal cells. In respond to osmotic shock and increasing salinity stress, algal cells increase the concentration of proline, mannitol, glycerol, and glycine betaine within cells and reduce the total chlorophyll and protein.^[35]

Phytoplankton biomass and the related primary productivity (PP) in many marine ecosystems are regulated by nitrogen (N) and/or phosphorus (P) availability. So, the composition and frequency of the phytoplankton populations is dependent on the nitrate and phosphate residual in a region. It has been observed

that, in a freshwater system, a reduced diatom population in the aquatic environment is indicative of changes in phosphorus in the environment.^[36] Climate change and related increased storm activity and rainfall may result in excessive run off of nutrients to the ocean and this could lead to eutrophication. Eutrophication can cause algal blooms and in the process favor some algal species over others, especially in coastal regions.^[37] Thus, the appearance of some algal species and also variations in dominance, diversity, and size of the algal populations could be utilized as bioindicators. For example, the diversity and appearance of fresh versus polluted populations of *Cocconeis placentula* and *Pinnularia microstauron* could serve as bioindicator of water quality.^[38] Moreover, measurements of the activities of some enzymes involved in regulation of nitrate and nitrate, such as nitrate reductase, could be developed as biomarkers for the evaluation of nutrient availability in aquatic environments.^[39,40] It is worth mentioning that many algal blooms involve species that can produce toxins which are harmful to human health and ecological conditions.

In general, algae are a suitable choice to be used as a bioindicator for the assessment of climate changes. The fitness of algal species both at the population level and individual level is due to: 1) high diversity in different environmental conditions; 2) high adaptability to climate changes in different ecosystems; and 3) high distribution rates and short life cycle. Related evidence of past climatic conditions can be gathered by carefully analyzing sediments and fossilized remains of algae.^[20] Since some factors such as pH, salinity, and trace metals have significant effects on the growth of algae, evaluating their effects is a potentially easy way to track the environmental conditions that are related to climate change.

2.2. Responses of Algal Communities to Physico-Chemical Stresses Associated With Climate Change

The interaction between living organisms and the physico-chemical conditions on our planet is delicate and minor fluctuations severely change this equilibrium. On the other hand, biological and non-biological processes regulate net air-sea flux values for natural and anthropogenic CO₂, so the climate processes should be studied as part of a complex matrix. Some organisms, including many algal species, have adapted to the afore-mentioned environmental stresses during their evolution.^[41] They can also evolve to cope with unfavorable conditions to enhance their growth. These evolutionary changes can include alterations in metabolic pathways and also changes in cell structure which are the result of genetic adaptation. Possible responses of phytoplankton populations to the afore-mentioned changing environmental properties are depicted in **Figure 2**.

The effect of doubling man-made CO₂ concentration due to the global Industrial Revolution has driven acclimatization in photosynthetic organisms. In some species of microalgae such as *Chlorella* sp., *Spirulina* sp., *Chlamydomonas* sp., *Dunaliella* sp., and *Nannochloropsis* sp. the consequences of such events were mitigated because of their efficient CO₂ sequestration mechanism and high amount of biomass production.^[42] Different species of algae show a wide range of tolerance to different

concentrations of CO₂ (**Table 1**). At the molecular level, studies have shown an improvement in electron transfer associated with photosystem I (PSI) under high concentrations of CO₂.^[43] Moreover, in green algae high concentrations of CO₂ lead to increased expression of carbonic anhydrase (CA) genes.^[44] It could be concluded that dissolution of CO₂ in ocean water has led to the increasing availability of inorganic carbon for phytoplankton communities. However, the ongoing acidification of ocean water has limited the nutrient availability in large oceanic regions. In fact, enhanced stratification caused by warming will make nutrient limitation stronger.

Marine systems and their biota suffer from another set of climate change effects caused by pH changes: algal communities are also influenced by ocean acidification. They respond to the related stresses in single cell and population level.^[45] pH plays an important role in availability of some essential nutrients and CO₂. Acidic pH leads to accumulation of toxic metals in algal cells, which could be deleterious to algal growth.^[46] Algal cells suffer from simultaneous exposure to acidic stress and stress from toxic metals because an acidic pH enhances solubility of metals, so an increasing concentration of these ions would be expected in acidic conditions. On the other hand, pH changes influence the absorption of some nutrients such as nitrate, nickel, etc.^[47] The pH also has a significant impact on the growth of algae in the water through altering the availability of carbon and nutrients, the activity of some enzymes and production of some algal bio-compounds in the cells.^[48]

In the oceans, a reduction in pH is mainly caused by the increased dissolution of CO₂ in the water. In these conditions, algae are able to increase photosynthesis through the intracellular supply of inorganic carbon.^[49] HCO₃⁻ is the major form of carbon in alkaline pH and the availability of CO₂ is limited. Many algae are also able to continue their photosynthesis in alkaline pH (pH10.8) due to systems involving the active transport of HCO₃⁻. This increases the CO₂ concentration at the active site of the CO₂-fixing enzyme ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (RuBisCO) within the cells. In some cases, these CO₂ concentrating mechanisms (CCMs) involve the activity of an external enzyme, CA.^[50] The external CA leads to an increase in the dehydration of HCO₃⁻ to CO₂ at the cell surface and consequently improves the supply of CO₂ for transport across the plasmamembrane in alkaline pH.^[51] Another mechanism involved in inorganic carbon adsorption is carried out through proton pump called vanadate-sensitive H⁺ATPases.^[52] According to the conclusion drawn by Reusch,^[53] adaptation to ocean acidification in any macroalgal community has not still been reported yet and macroalgae appear not to have evolved ways to tolerate this pH stress. However, limited studies show a switch from calcifying species to non-calcifying macroalgae in area of volcanic CO₂ seeps, since the newly introduced species cope better with the acidified conditions.^[54] On the other hand, many microalgae are able to grow in acidic conditions. Algal cells are able to provide appropriate responses to acidic conditions. For example, low conductivity of the plasma membrane to H⁺ improves the buffering capacity in the cell, as well as improving the capacity of cells to transfer H⁺ to the extracellular environment to reduce proton concentrations inside the cells.^[55] Moreover, cells can produce some enzymes such as H⁺-ATPase and extracellular acid phosphatase enzymes

Physiological response	Environmental condition				
	Ocean acidification	Increased temperature	Enhanced stratification	Increased salinity	Decreased light penetration
Photosynthesis					
Reproduction					
Calcification					
Nutrient biofixation					

Figure 2. Possible responses of habitat phytoplankton population to changing environmental properties.

which could enhance the tolerance to acidic conditions in some algae.^[56]

The algal strains that are able to survive in acidic conditions should also have the ability to grow in high concentrations of trace metals.^[57] These strains produce compounds in the cell that control the development of tolerance to trace metals by binding to.^[58] For example, phytochelatins have been identified in algae and play an important role in the detoxification of trace metals.^[59] Phytochelatins are glutathione oligomers that are produced by reactions involving the enzyme phytochelatin synthase. Thiol groups are also involved in this process. Binding of metal ions to glutathione leads to increased production of phytochelatin synthase that occurs in the presence of heavy toxic metals.^[59] Metallothioneins also have the same role in detoxification of toxic metals in algae. Metallothionein is rich in cysteine and due to the thiol groups in the cysteine molecules can bind to trace metals. Metallothioneins are involved in the absorption, transfer, and adjustment of different toxic metals in the cells.^[60]

Ocean temperature can bring about changes in the productivity and composition of marine phytoplankton.^[61] Global warming imposes a combination of positive and negative effects on algal cells: Changes in temperature lead to changes in biochemical and morphological features as well as growth rate of affected algal communities; however, algae are able to adapt to temperature changes in different biogeographic regions.^[62] For example, the green alga, *Chlorella vulgaris*, showed an increase in growth rate, chlorophyll content, and biomass in warmer condition up to 30 °C.^[63] Similar responses were reported for cultivation of *Chlorella* sp. and *Chaetoceros calcitrans*.^[64]

Algal cells may also respond to temperature variation through changes in the level and composition of fatty acids in their plasmamembrane. Studies have also shown that increasing temperature to 38 °C leads to the accumulation of oleic acid as a mono-unsaturated fatty acid within the algal cells^[65] and, as a result, a more flexible cell membrane could improve the stress tolerance in adapted algal strains. In addition, temperature influences carbon flux and also starch content of marine algal cells; increased temperature leads to degradation of the starch, as shown in a study by Goldman et al.^[66] on *C. vulgaris* where it was observed that high temperature caused a significant decrease in starch content with attendant increase in sucrose. In a study of

the effects of different temperatures on growth and photosynthesis in ten strains of the cyanobacterium *Synechococcus* sp, resistant cells increased the abundance of pigment-protein complexes in the phycobilisomes, some subunits of PSI, PSII, and the cytochrome *b₆f* complex at high temperatures. These changes consequently help maintain the photosynthetic rate and prevent damage to PSI at higher temperatures.^[67] Secretion of abscisic acid as a consequence of increased temperature in the green alga, *C. vulgaris*, has been reported to be effective in the control of growth responses and regulation of responsive genes.^[68]

Numerous reports have repeatedly confirmed the potential of algal communities to respond and also adapt to global warming. Based on the presence of macroalgal thermal ecotypes in different geographically widespread regions, Eggert suggests that local adaptation to the prevalent temperature regime would be possible.^[69] Another example of biogeographic distribution patterns was found by Rowan^[70] in adapted stony corals of the genus *Pocillopora*, hosting resistant warm-water endosymbiotic dinoflagellates *Symbiodinium* sp. These observations indicate that if other coral species living in frequently warm habitats (>31.5 °C) can host similarly resistant strains, corals might adapt to warmer habitats and better cope with global warming.

The fingerprint of acclimatization to different environmental factors can be found in different algal strains. More examples are summarized in Table 1.

Salinity can affect various aspects of marine life. Increasing concentration of salt in the medium leads to formation of an osmotic gradient which causes cells to lose water. Moreover, some toxic ions such as chloride may interrupt normal cell growth.^[112] Salinity can also affect the solubility of various gases such as CO₂ in the oceans.^[113] Moreover, salt concentrations affect photosynthesis and respiration rates in algae^[114] and inhibit cell division and production of biomass.^[115] Some algal strains naturally have the ability to grow in hyper-saline water. For instance, *Dunaliella salina* shows increased photosynthesis rate, cell division, and growth rate at high salinities.^[76]

Marine microalgae can respond to salinity stress using different adaptation mechanisms. Alterations in metabolic fluxes, keeping the K⁺/Na⁺ balance within the cell, accumulation of K⁺ ions with ejection of Na⁺, and accumulation of pigments such as β-carotene are among the robust mechanisms

Table 1. Responses of algal strains to physicochemical stresses, from climate change, in the marine environment

Environment condition	Consequence	Acclimatization of some algal strains	Phylum	Algal response type	Research area	Reference		
Increased CO ₂ concentration	Global warming; ocean acidification; sea-level rise; increased drought and tropical storms	<i>Chlorella</i> sp.	Chlorophyta	Accumulation of lipid; change in CCM mechanism; stimulation of plasma membrane ion anti-porter system; down regulation of CA gene activity; changing calcite deposition	Laboratory investigation	[71–77]		
		<i>Nannochloropsis</i> sp.	Ochromytha		Provided from Mercian, Japan laboratory investigation			
		<i>Scenedesmus</i> sp.	Chlorophyta		Laboratory investigation			
		<i>Chaetoceros</i> sp.	Bacillariophyta		Algae isolated from the southern Atlantic Ocean water			
		<i>Ulva rigida</i>	Chlorophyta		Algae isolated from intertidal rocky shore in Málaga, Spain			
		<i>Gracilariopsis chorda</i>	Rhodophyta		Algae isolated from the Wando Island, Korea			
		<i>Spirulina</i> sp.	Cyanophyta		Indian Agriculture Research Institute, New Delhi, India, laboratory investigation			
		<i>Porphyra seriata</i>	Rhodophyta		Laboratory investigation, Korea	[78–85]		
		Increased temperature	Melting glaciers and ice sheets, increased sea level; increasing the salinity of wetlands, rivers and oceans; changes in oceanic current systems; increasing mortality in marine ecosystems	<i>Scenedesmus obliquus</i>	Chlorophyta	Change in the level and composition of fatty acids in plasma membrane; changes in chlorophyll content and photosynthesis; increasing the content of pigment proteins, such as phycoerythrin; regulation of responsive genes such as HTR and Hsp genes; eutrophication	Laboratory investigation, the University of Texas culture collection of algae	
				<i>Chlorella</i> sp.	Chlorophyta		Laboratory investigation	
<i>Fucus vesiculosus</i>	Ochromytha				Collected from the non-tidal Kiel Fjord, western Baltic Sea			
<i>Phyllophora pseudoceranoides</i>	Rhodophyta				Zone of Helgoland, North Sea			
<i>Polyides rotundus</i>	Rhodophyta				Zone of Helgoland, North Sea			
<i>Tetraselmis</i> sp.	Chlorophyta				Isolated from coastal seawater of the Yellow Sea in Incheon, Korea			
<i>Chlamydomonas reinhardtii</i>	Chlorophyta				Laboratory investigation	[86–97]		
Light budget variation	Improving function of the photosynthetic apparatus and changing its efficiency and related carbon fixation capacity; conservation of benthic organisms and primary production of the oceans; changing temperature of					Accumulation of mycosporine-like amino acids and photoprotective pigments; improved biomass production; increased production of carotenoids; changes in the expression of some effective proteins in light harvesting antenna; activation of kinase; inhibition of		

(Continued)

Table 1. (Continued)

Environment condition	Consequence	Acclimatization of some algal strains	Phylum	Phototaxis	Algal response type	Research area	Reference
various layers of water in the oceans and the stratification	Changes in the density of seawater and ocean water; change in freezing point of water; effective on the oceanic current and the water cycle; effective in the event of flood and drought	<i>Enteromorpha</i> sp.	Chlorophyta	Phototaxis	Increasing K^+ and Ca^{2+} concentration inside the cells and also Na^+ ejection, maintaining the K^+/Na^+ balance inside the cell using the stimulated plasma membrane ion anti-porters; expressing cytosolic apoaquorin; increasing lipid concentration in intercellular space; up-regulation of some transports genes such as K^+ transporters as well as glutamate and praline synthesis; changes in glycerol concentration in the cell; change in cell volume	Collected in a beach near the Mondego estuary-Figueira da Foz, Portugal, laboratory investigation	[76,98–104]
		<i>Botryococcus</i> sp.	Chlorophyta			Isolated from a freshwater reservoir in central Thailand	
		<i>Microcystis aeruginosa</i>	Cyanobacteria			Isolated from Jacarepaguá Lagoon, Brazil	
		<i>Heterosigma akashiwo</i>	Ochrophyta			Isolated from the mid-Atlantic of the United States	
		<i>Undaria pinnatifida</i>	Ochrophyta			Collected from the coast of Dongbak Island, Busan, Korea	
		<i>Prorocentrum minimum</i>	Dinophyta			Isolated from the inland bays of Delaware	
		<i>Anabaena</i> sp.	Cyanophyta			Laboratory investigation	
		<i>Dunaliella</i> sp.	Chlorophyta			Laboratory investigation	
		<i>Scenedesmus quadricauda</i>	Chlorophyta			Isolated from the fresh water pond of village Ladwi, Haryana, India	
		<i>Chlorococcum submarinum</i>	Chlorophyta			Laboratory investigation	
pH variation	Decrease the CO_2 absorption capacity in low pH; effective on calcifying species through decreased carbonate ion; deformation of shells and skeletons; reducing coastal rocks protection and increasing erosion due to damages to	<i>Microcystis aeruginosa</i>	Cyanophyta	Changes in the structure and content of cellular skeletons in some algae (changes in the concentration of crystals for the calcification of cellular skeleton); changes in cell morphology; change in growth rate; antioxidants production; regulating the	Collected from the Institute of Hydrobiology (FACHB), Chinese Academy of Sciences, China	Isolated from the West coast of India	[105–111]
		<i>Lyngbya confervoides</i>	Cyanophyta				

(Continued)

Table 1. (Continued)

Environment condition	Consequence	Acclimatization of some algal strains	Phylum	Algal response type	Research area	Reference
	coral reefs, endangering the food chain web in the oceans, food and jobs			expression of some genes such as Hsp, and the activity of certain antioxidants, such as superoxide dismutase; increasing activity of Ca ²⁺ and HCO ₃ ⁻ transporter at pH 7.5; increasing secretion of organic matrix protein; preserving saturation of argonite in the cell for the calcification process; oxidative phosphorylation	Isolated from the West coast of India The Phycology Lab, Faculty of Science, Zagazig University, Egypt, laboratory investigation	
		<i>Chroococcus turgidu</i> <i>Spirulina platensis</i>	Cyanophyta Cyanophyta		Collected from field sites on the West Florida Shelf	
		<i>Halimeda</i> sp.	Chlorophyta			

that are stimulated in cells faced with salinity stresses.^[76] Accumulation of compatible solutes can enhance the tolerance of algal cells to environmental stress. Osmoprotective compounds are among the metabolites that protect the cells against oxidative stress or high concentrations of inorganic ions.^[116] Stimulation of pathways associated with inhibition of reactive oxygen species (ROS) could be considered as another mechanism that could improve the cell resistance to abiotic stress caused by salinity.^[117] To cope with the negative side effects of salinity, some algae change the net charge of some amino acids to be able to maintain hydration during stress.^[118] Transcriptomics studies have confirmed an increase in the expression of some genes such as Hsp90 and β -tubulin during the dehydration process. Activity of these genes is stimulated by salinity stress in many algae such as *C. vulgaris* and *Asterochloris* sp.^[118]

Some secondary metabolites within the algal cells act as antioxidants. Antioxidants act as radical scavengers, preventing the degradation of electron transport chain components in cell membranes, as well as breakdown of major metabolites in the cytoplasm.^[119] Murugan and Harish^[120] evaluated the accumulation of some antioxidants in response to induction of oxidative stress in *Cladophora glomerata*. They showed that lipoperoxidase activity positive correlated with the accumulation of trace metals. Increased activity of ascorbate peroxidase and superoxide dismutase also confers resistance against oxidative stress. Moreover, Sunda et al.^[121] investigated the role of dimethylsulfoniopropionate (DMSP) and dimethylsulfide (DMS) in resistance to oxygen free-radicals and ROS, and showed that the concentration of DMSP and DMS increases with increasing UV light, carbon limitation, iron limitation and increased Ca²⁺ and H₂O₂.

Finally, manipulation of some metabolic pathways can improve algae tolerance to unfavorable climatic conditions. However, in view of the few molecular studies to identify genes involved in metabolic pathways for the development of tolerance to climate changes in algae, our understanding of such strategies is still in their infancy. Identification of genes and transcription factors involved in the development of tolerance to abiotic stresses or climate change effects have been carried out using genome analysis and functional genomics approaches in algae.^[122] This is done by transferring stress-induced promoters and evaluation, and selection of tolerant algae or manipulation of key enzymes. The details of the new employed approaches in the system and synthetic biology is provided in the recently published studies such as investigation done by, for example, Ramos et al,^[123] Holzinger and Pichrtova,^[124] Im et al,^[125] and Wi et al,^[126] etc.

In conclusion, climate change and related thermal effects from rising global temperatures have resulted in melting glaciers which alter salinity, and ocean acidification which has further led to increased levels of dissolved toxic metals and accumulation of other chemical contaminants in the ocean.^[127] These contaminants adversely affect the survival and sustainability of the ocean food chains.

Some studies have considered the capacity to use algae to clean up contaminated marine water.^[128] Algal communities can potentially mitigate the previously discussed impacts of climate changes on ocean ecosystems. This potential to ameliorate

climate change will be introduced in detail in the following sections.

3. Mitigation of Climate Change Using Algae

Today, the world is facing climate change and global warming caused by human and related industrial activities. This leads to changes in the physical and chemical features of hydro-sphere.^[129] Considering the large role of marine phytoplankton in global biomass production (about 50% of the total PP),^[130] there is a potential to gain from ability of algal communities to mitigate the consequence of climate change.

Generally speaking, algae could play an important role in the transfer of atmospheric carbon to blue carbon reservoirs in the oceans.^[131] However, the afore-mentioned abilities of algal strains to cope with environmental stresses do not mean that algae could answer all the challenges faced in climate change but instead to show that there is a potential for algae to be used in carbon bio-sequestration strategies.

3.1. Enhancement of Biological Carbon Sequestration

The process of photosynthesis by photoautotrophic organisms is one of the most important ways for CO₂ sequestration to occur.^[132] Biological sequestration of atmospheric and hydrospheric carbon by algae and cyanobacteria could lead to efficient and affordable CO₂ reduction in the biosphere.^[133] In biological carbon sequestration, plants, algae, and cyanobacteria absorb carbon from the atmosphere as well as the euphotic zone in aquatic ecosystems and this finally leads to carbon accumulation in the biomass of photoautotrophic organisms. Consequently, a portion of the absorbed carbon in biomass sinks (in aquatic systems) or contributes to soil organic compounds, fossil fuels (in the long term), and sediments.^[134] The contribution of fixed CO₂ depends on how easily the organic matter is broken down. For example, macroalgae can release 20–40% of their productivity in the form of dissolved organic matter (DOM).^[135] A large portion of DOM in macroalgae can be degraded by microbial activities.^[131] UV radiation is also another factor in the destruction of DOM, but this degradation process is reduced in the depths of the oceans where there is less light.

Several studies have shown that algae are organisms that have high growth potential and efficient photosynthetic apparatus, and are much more capable of carbon sequestration compared to other organisms^[132,136,137]; the efficiency of CO₂ fixation in algae is 10–50% higher than terrestrial plants.^[138] CO₂-fixation in algae is associated with the production of energy containing compounds and this could, in turn, positively influence the feasibility and economics of algal-bioenergy production.

Basic knowledge of system biology and also studies of metabolic pathways would throw light on the identification of some regulating genes involved in important cell functions. In the case of CO₂ sequestration capability of algal cells, introduction of or improvements to carbon concentration mechanisms (CCMs) could not be neglected. Although most algae and cyanobacteria possess a capacity for CCMs, the next

step could be implementation of genetic engineering techniques to improve the native potential.

CCMs could be exploited to increase algal photosynthesis efficiency as well as their growth rate.^[139] Several studies have shown that many microalgae express CCMs to utilize dissolved inorganic carbon (DIC), such as HCO₃⁻ and CO₂.^[140,141] This ability increases the CO₂ concentration within the cells and consequently it leads to improved photosynthetic activities of the algae in a low external concentration of CO₂ as it accumulates CO₂ at the active site of RuBisCO.^[142] As a result, net photosynthesis (CO₂ assimilation) increases and photorespiration (carbon oxidation) ceases. Activity of external CA, as an important enzyme in some CCMs, could lead to an increase in the rate of photosynthesis in algal cells.^[143,144] External CAs also increase the use of inorganic carbon in the form of HCO₃⁻.^[145] In brief, external CA activity leads to increased CO₂ concentrations at the plasma membrane caused by the dehydration of HCO₃⁻.^[146] In addition, ATPase could also increase the CCM efficiency. ATPase causes an electro-chemical proton gradient in the plasma membrane and generates an acidic condition in the lumen of photosynthetic organisms.^[140] Acidic conditions occur due to the conversion of ATP to ADP and H⁺ accumulation in the target sites. It is essential for HCO₃⁻ dehydration and CO₂ accumulation to improve the activity of the RuBisCO.^[147] Specific transporters are essential for the transport of inorganic carbon and photosynthetic activity in algae.^[148] These transporters are very useful when there is a high alkaline and high saline condition (such as seawater) because the unanalyzed formation of CO₂ from HCO₃⁻ is slower in such conditions. In a study on the diatom *P. tricornutum* the activity of a series of plasma membrane transporters directly correlated with improvement of the absorption of DIC and photosynthetic activity due to their role in facilitating the acquisition of CO₂.^[149]

In brief, CCMs are only effective if the CO₂ concentration is at air equilibrium or below. Their expression is down-regulated as CO₂ levels rise and where there is low light; so, although researchers have been looking at using CCM functions to improve CO₂ fixation, over expressing CCMs in algae is unlikely to be very effective. However, the introduction of involved genes in this mechanism to organisms that currently lack them, for example, some sub-tidal red algae, Chrysophytes, and the green alga *Coccomyxa*,^[139] could increase the carbon sequestration capacity.

Some aspects of the process of accumulation of DIC within algal cells using CCMs have been targeted for improvement by genetic/metabolic engineering to enhance the biological carbon sequestration ability of some algal species. The higher the capacity for carbon sequestration, the faster the doubling time would be and such algal strains could be implemented to mitigate global warming caused by GHGs emission. For example, introduction of a system to express and secrete CA in the cyanobacterium *Synechococcus elongatus* improved the yield of CO₂ assimilation.^[150]

Manipulation of algal capacity for CO₂ sequestration is not restricted to application of genetic engineering approaches. Several microalgal cultivation systems have been proposed for enhanced CO₂ sequestration, among them open pond systems and closed photobioreactor systems will be discussed in detail here. There is much discussion about which of these systems is

better for CO₂ sequestration. Obvious advantages of the open pond system are low initial and operational costs. On the other hand, an advantage of the photobioreactor system is the higher production due to better control of environmental conditions and optimum harvesting efficiency. The major disadvantage of an open pond system is that it requires a large area to sequester significant amounts of CO₂. However, the higher initial investment is a disadvantage of closed photobioreactor systems.^[151]

Open pond systems are closed loop channels with depth of 20–30 cm that are often covered with transparent plastic. Paddle wheels are installed to maintain turbulent flow of water. Generally, in this system there is a high contact surface and open ponds could absorb more sunlight.^[152] On the other hand, a closed photobioreactor system operates in the same way as fermentation vessels and requires CO₂ and light to be provided. Most of these systems are in the form of a tube, vertical columns, or rings and they provide proper circulation of medium culture.^[153] In addition, offshore cultivation of seaweeds is also possible. In this system, algae cultivation is done in inshore coastal regions or in shallow ponds.^[154]

3.2. Algae-Derived Low-Carbon Bioenergy

The energy crisis threatens the future of humanity from two perspectives: 1) reduced fossil fuel resources; and 2) degradation of environmental conditions and pollution of natural resources. Consequently, replacement of fossil fuels with green fuels is very important and alternative, green, fuels such as biofuels are under development. Bioenergy supply if not carbon neutral, will need to be low-carbon. If sufficiently low carbon feedstock can be sourced, bioenergy has a potentially useful role in meeting carbon budgets.^[155]

Biofuel produced by crops faces many problems such as low carbon acquisition efficiency, poor life cycle emissions and a requirement for large amounts of land and fresh water; all these have darkened the future of green fuel production.^[156] Environmental friendly aspects of algae-derived bioenergy could circumvent such negative impacts of biofuel production from crops because algae-based fuels offer a wide range of advantages; algal cultivation has developed with the benefits of faster assimilation of nutrients from waste effluent, year-round production, and higher photosynthetic yield and these features allow cultivation of microalgae using non-potable water resources and agricultural wastewater,^[157] Moreover, the production of energy-rich compounds in algal cells could be enhanced using newly emerged genetic engineering tools. The potential of engineered algae to be used in low-carbon strategies for biofuel production is summarized in **Figure 3**. Large-scale methodologies are based on the relationship between synthetic biology and other upstream considerations.

Photoautotrophic microalgae are capable of generating various types of biofuels, while simultaneously promoting CO₂ fixation during their growth. For example, supplementation of up to 20% CO₂ in the air stream of cultures of *C. vulgaris* and *Botryococcus* sp. strains provide higher oil yields with enhanced

biodiesel properties.^[158] Under optimal nutrient-replete growth conditions, algal cells can utilize the simple inputs from wastewater to increase biomass accumulation and this further causes biofuels to be more sustainable.^[138,159] Therefore, the use of algae can resolve concerns of declining fossil fuel resources and climate changes.

In general, there are four main pathways for converting algal biomass to biofuels: 1) transesterification of triacylglycerol (TAG) for biodiesel production; 2) fermentation of carbohydrates for bio-alcohol production; c) anaerobic digestion for biogas production; and 4) gasification.^[160]

3.2.1. Biodiesel

Biodiesel is routinely produced from lipids accumulated by crops and potentially so from algae, though the latter is currently economically unfeasible. Due to the use of lipids in crops as food, using algal cultivation to obtain biodiesel is, however, potentially attractive. On the other hand, the cultivation of algae for biodiesel production requires to less space for cultivation than oil plants.^[161] For example, Chisti^[162] suggested that algae with around 20% lipid content would be able to produce 3–30 tons oil/ha per year, which is 60 and 30% higher in comparison to soybeans and rapeseed, respectively.

Algae are able to store large amounts of free fatty acids in the form of TAG in the cell. TAGs can be used as the primary material for biodiesel production. This substrate is converted into biodiesel during the transesterification reaction.^[163] Different species of algae are potentially suitable for biodiesel production such as *C. vulgaris*,^[164] *D. salina*,^[165] *Nannochloropsis* sp.,^[166] and *Botryococcus braunii*.^[167] Genetic engineering techniques are extensively implemented to enhance the yield of biodiesel production. For example, researchers now are able to stimulate the algal cells to produce more fatty acids with a desirable profile which could be easier to extract without the complex pretreatment steps.^[168,169]

3.2.2. Bio-Alcohol

Since the efficiency of photosynthesis in algae is higher than in crop plants, algae can accumulate high amounts of carbohydrates using freely available inputs.^[170] Their cell walls and starch in the plastids are virtually free of recalcitrant structural biopolymers such as lignin and hemicelluloses, so they can be readily converted into fermentable sugars without using energy-consuming pretreatment steps.^[171] Genetic manipulation approaches have been investigated to achieve the goal of sustainability of the process by direct production of bio-alcohols in live algal cells.^[172]

3.2.3. Biogas

Anaerobic fermentation of algae biomass for recycling and utilization of biomass energy is very important for biogas (such as methane) production. In addition, controlled anaerobic

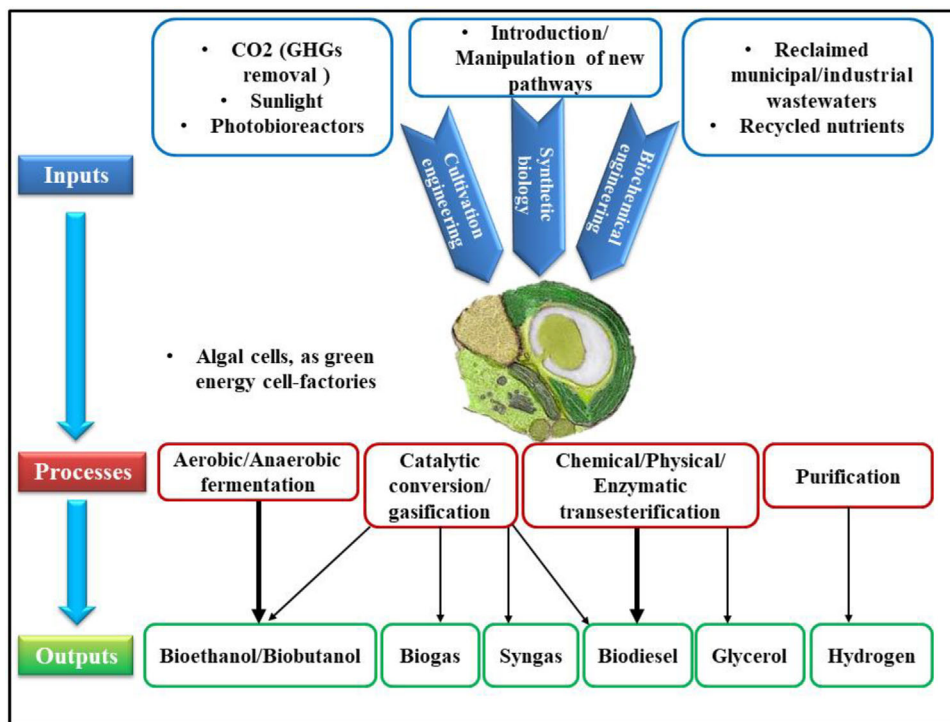


Figure 3. Schematic diagram representing framework to channel captured energy in photobiosynthesis into biofuels using engineered algae cells.

digestion can promote the treatment of environmental wastewater and reduction of GHGs by decreasing the burning of fossil fuels.^[173] The production of biogas in algae has a higher efficiency compared to crops.^[174] Generally, algae biomass remains can be used to produce biogas after extraction of lipid and fermentation of sugars.

3.2.4. H₂ Production

Hydrogen gas has the potential to produce clean energy for transportation and power generation. Freshwater green algae such as *Chlamydomonas reinhardtii* and *Chlorella fusca* are organisms that metabolize H₂ under anaerobic conditions. However, in a sulfur-free environment, *C. reinhardtii* produces H₂ in the process of photosynthesis instead of producing O₂. This gas can be used as a clean fuel.^[175] During the process of photosynthesis, H₂ is produced by proton reduction catalyzed by the hydrogenase enzyme. Moreover, light absorption is essential for the production of H₂ gas; the energy of sunlight is used for hydrolysis and the released electrons are transferred to ferredoxin. Ferredoxin makes it possible to transmit electrons to Fe ions in the hydrogenase enzyme.^[176] Of course, the sensitivity of the hydrogenase enzyme to oxygen could make H₂ production less sustainable. Today, genetic engineering techniques are used to overcome the difficulties of the process through increasing resistance of the hydrogenase enzyme to O₂, maintaining the proton gradient across thylakoid membranes and also overall improvement of the photosynthetic capacity of the algal cells.^[177,178]

4. Conclusions

In conclusion, the oceanic CO₂ concentration is regulated by a set of complex interplays of different physical, chemical, and biological processes, affecting net air–sea flux values of natural/anthropogenic CO₂ positively and/or negatively. The uncontrolled release of CO₂ into the atmosphere in a very short time frame has imposed changes to the global heat budget, light penetration, atmospheric, and hydrospheric currents as well as physico-chemical properties of the oceans. These factors consequently have a great influence on the driving forces for carbon sequestration in the oceans as a sink for anthropogenic CO₂. Algal communities as players in the carbon sequestration process in the oceans are influenced by the afore-mentioned changes. Among them, increasing temperature, varying pH, and also limited light supply directly influence photosynthetic phytoplankton. However, some algae not only possess an ability to grow in potentially inappropriate conditions but also have the capacity to deal with many environmental pollutants such as CO₂, nutrient-rich wastewater, trace metal pollutants, etc. In addition, algae are able to produce value-added materials such as biofuels, pharmaceutical compounds, and antioxidants. These species can also be used as bioindicators for identification of various climatic changes. For these reasons, the identification of various algal species that thrive in response to climate change would be helpful.

Our limited understanding of the feedback mechanisms that affect the biology of the oceans and the predicted oceanic responses to climate change (e.g., dramatic pH variation, temperature increases, changes in stratification and circulation,

light and nutrient supply), highlight the importance of further comprehensive studies of climate change effects on the life in the oceans. All these complex responses make it difficult to assess how the biological pump will react to future climate changes and one cannot assume that the steady-state operation of the carbon cycle will continue forever. The biological pumps are interacting with likely consequences of climate changes in oceans and the assumption of a steady-state oceanic carbon cycle during the 20th century must now be re-evaluated.

Abbreviations

CA, carbonic anhydrase; CCM, carbon concentration mechanism; DIC, dissolved inorganic carbon; DMS, dimethylsulfide; DOM, dissolved organic matter; GHG, greenhouse gas; HSP, heat shock protein; IPCC, Intergovernmental Panel on Climate Change; PP, primary productivity; PSI, photosystem I; ROS, reactive oxygen species; RuBisCo, ribulose-1,5-bisphosphate carboxylase/oxygenase; TAG, triacylglycerol; UV, ultraviolet.

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Conflict of Interest

The authors have declared no conflict of interest.

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