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ORIGINAL ARTICLE

Algae: the world's most important "plants"—an introduction

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Abstract Early in the history of life, algae changed the planet's atmosphere by producing oxygen, thus paving the way for the evolution of eukaryotic organisms. In an era in which the consumption of fossil fuels is a prime topic of concern, few people realize that the oil we currently exploit comes mostly from Cretaceous deposits of marine algae. Moving from ancient times to the present, the algae remain more important than most people realize. Today, the production of oxygen by algae (ca. 50% of all oxygen production) is another reason for saying "our lives depend on algae." Those who love seafood should thank the algae because algae are the primary producers upon which aquatic ecosystems depend. Thanks should come from all who are vegetarians or omnivores, because all land plants derive from a freshwater class of green algae and all land-animals—including the cows that provide the steaks for meat-lovers—depend directly or indirectly on land plants for food and often for shelter as well. As we use up the oil deposits provided by the ancient algae, we are turning to the modern algae for help. Given the photosynthetic abilities of the algae, they are one of the major focuses for sustainable biofuel production and CO_2 consumption. Finally, the algae that give us the air we breathe, the food we eat, and the fuel for our cars (past and, perhaps, future), are also a source of active pharmaceutical compounds that can be used against drug-resistant bacterial strains, viruses (including Herpes Simplex and AIDS), and cancers. Roses are pretty and oak trees are impressive, but no other groups of "plants" have done so much, for so long, and, for so many as have the algae!

Keywords Algae · Biofuels · Food · Oxygen · Pharmaceuticals · Land plant evolution · Sustainable fuels

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1 Introduction

Algae and attitude Most people are not at all aware of the importance of algae. This lack of appreciation of the world's most important plants is not surprising, at least among English-speaking populations. Consider the common names used for the algae: pond scum, seaweeds, and even frog spittle! Indeed many people only experience algae in "bad situations" such as a big problem in local lakes, fishing holes, or even personal swimming pools, or as insect-covered seaweed litter on the beach or as contaminants in tropical fish tanks, or even worse, as red tides poisoning our seafood and/or us. Perhaps there is no wonder about why more people have never, ever taken a phycology course to understand the plants upon which their lives totally depend. This article will, one hopes, serve as a mini-phycology course that will provide just enough background information to give the reader who has very little awareness about algae a basic appreciation of what they are and how tremendous the variation in size, habitat, and "life style" among algae is. Thus, when one encounters the mounting mass of articles about algae and biofuels or algae and carbon capture, etc., there will a context for understanding which algae are being proposed to do what functions.

Now no one likes to begin an overview article on an important topic with a controversy and I will avoid controversy by explaining I have placed the word "plants" in the title in quotes to avoid or at least minimize controversy. Some people would argue (strongly) that "plants" are only the land plants we all commonly think of as plants (the bryophytes—mosses, liverworts, and hornworts, pteridophytes—ferns and fern allies, gymnosperms—conifers and their kin, and angiosperms—the flowering plants). Others would say molecular evidence shows clearly that the green algae (i.e., the Chlorophyta) and the land plants are plants, but no other algae are. Others, also citing molecular evidence, would say that the red algae (i.e., the Rhodophyta) are also "plants." But to extend the term "plants" any further, beyond the land plants, green algae, and red algae, may be very troubling (horrifying) to some. The vexation caused might reach its peak over calling the blue–green algae plants—in fact there is even controversy about calling them blue–green algae rather than cyanobacteria (despite the fact that the former term is more colorful). Well, often controversies rage simply because people accept different definitions of terms (and actually have no real basis for quarrel at all beyond the definitions). Thus, to avoid even a hint of controversy, the working definition of "plants" for this article is as follows: organisms that contain chlorophyll *a* and perform oxygen-producing photosynthesis (and their colorless close relatives [e.g., *Astasia* is thought of as a colorless *Euglena* that no longer has chloroplasts]). With this definition the blue–green algae can remain truly cyanobacteria but we can call them plants. And we do not have to say that the magnificent, giant, plant-like kelps are not plants. Clearly, those who cannot abide this working definition of "plants" can simply use whatever definition they prefer in their own writings, and forgive me for using "plants" as a convenient term for this article.

Plan of attack This article will begin with a simple grammar lesson, comment on attitudes, discussion of some the major examples of the importance of algae, and a very brief introduction to some major groups of algae. It will then return to additional ways in which the algae are far more important to humankind than most humans realize.

2 Discussion

Grammar lesson You can have one alga, or, two or more algae, but you can never have "algas" (unless you are writing in Spanish or Portuguese that is). Despite the fact that recognizing "alga" is singular and "algae" is plural seems fairly simple, one has only to listen to the radio or to university lectures or read the papers to realize that seeing or hearing expressions like "Algae is an important source of biofuels." are probably here to stay (at least until all editors are forced to take Latin 101).

Algae and attitudes In the English language, the common terms for algae include "pond scum," "seaweeds," "rockweed," " bladder wrack," "sea wrack" and, even "frog spittle." Thus, the poor algae start off with a negative connotation as soon as we talk about them. Similarly, since most people do not learn about algae at all at any level of their educational history, awareness of the algae may derive from basically bad situations, such as news clips about poisonous red tides and shellfish poisoning, about masses of green seaweeds threatening Olympic sailing events in China, or from algal problems in their own swimming pool. Indeed when one hears or reads that the local fish-kill in the town lake was caused by a massive bloom of algae, one cannot escape thinking, "Algae are bad." In response to this erroneous notion, the subtheme of this article is, "Algae good, people bad" (at least as far as the environment is concerned). Though this mantra may be considered overly zealous on behalf of the algae, one can argue that the "pond scum" and "seaweeds" need a strong defense and the best defense is often an offence.

Olden times Some 3.5 billion years ago prokaryotic life began on the planet in the absence of oxygen. The cyanobacteria (blue–green algae) arose and began releasing oxygen into the atmosphere as the waste product of chlorophyll a-mediated photosynthesis. However, the levels of oxygen did not rise significantly for about a billion years. Why? Because exposed iron and other metals in surface rocks oxidized and consumed oxygen, and because the massive ocean absorbed oxygen. But about 2.45 billion years ago the level of oxygen in the atmosphere began to rise because the exposed minerals were fully oxidized and absorption by the oxygen-enriched upper layers of the ocean abated (Kump 2008). Oxygen levels rose and the evolution of eukaryotic organisms began, giving rise along the way to humans (for better or worse). For changing the atmosphere and the course of evolution, the blue–green algae deserve our thanks.

Modern times Algae in the oceans, rivers, and lakes of the world are thought to produce about half of all the oxygen produced on the planet. Those of us who appreciate breathing should offer the algae our thanks. Given that the total biomass of the world's algae is but a tenth of the biomass of all the other plants, the efficiency of the algae is impressive (and of interest in terms of producing biofuels—but more of that later).

Conquering the land Among the various eukaryotic organisms evolving in the oceans and lakes of the planet were various forms of algae, including the green algae (Chlorophyta). In the Paleozooic era perhaps about 480 million years ago (Wellman et al. 2003), a grand conquest occurred and yet this victory is not routinely celebrated by any nation on the planet! It was the conquest of the land by green algae and the evolution of the "real plants," that is, the land plants (including the bryophytes, ferns and fern allies, the gymnosperms, and the flowering plants). Since all land plants come to us *via* the green algae, every vegetarian and vegan should thank the algae. Of course, those of us who enjoy steaks and beef Wellington also should thank the algae because cows eat grass. While we are discussing food, it is important to note that those who like salmon, oysters, lobster, and every other form of seafood must offer their thanks to the algae, since the algae are the primary producers in aquatic ecosystems—the starting point in the food chain or food web and thus the *sine qua non* for the fine seafood some of us love. Man lives not by bread alone, so although we must acknowledge that the algae, in a sense, have given us all of our seafood and all of our "land–food," we have to thank them also for timber and fibers, for habitats, for beautiful flowers and beautiful forests…basically for life as we know it.

The major groups of algae Having acknowledged and thanked the algae for changing the earth's atmosphere and facilitating the evolution of us and other eukaryotes, for providing much of the world's oxygen each year, for providing all seafood and all "land food" for us and all other animals, and for all the habitats, products, and beautiful flowers we enjoy, it is time to introduce some major groups of algae. We will start with the big ones and then cover the little ones.

The big algae—the seaweeds Everyone who has spent time along the ocean coasts or around lakes and ponds, has noticed some of the big algae, or macroscopic algae and these easily visible algae are mostly three groups with simple, colorful names. They are the green algae, the red algae, and the brown algae (or the Chlorophyta, Rhodophyta, and Phaeophyta respectively). Books can be, and have been, written about each group, but just a few essential facts will serve as a quick introduction to each group.

Green algae (Chlorophyta) There are an estimated 6,000 to 8,000 species of green algae (and one should remember the number is truly just an estimate) and ninety percent of them are freshwater rather than marine. As mentioned above, a freshwater green algal ancestor conquered the land and gave rise to the land plant flora, in fact the green algae are in a monophyletic (or natural) group with the land plants. The green algae and the land plants all share a common ancestor, and, all descendants of that common ancestor are either green algae or land plants. Although many of the green algae are large (macroscopic) seaweeds, they can also be tiny unicellular or colonial organisms. Some marine green algae are truly sea "weeds" and one beautiful green alga, *Caulerpa*, is known as the "scourge of the Mediterranean" where it is a highly invasive weed introduced by accident in Monaco in 1984 just beneath the Oceanographic Museum (Meinesz et al. 2001). A less beautiful green alga, *Codium* ("deadman's fingers"), has been invading the east coast of the U.S., steadily moving northward and plaguing already plagued shellfish industries along the way. Given these examples of invasive species, the question arises: Are these algae bad? The answer is a resounding, "No!" Humans deliberately or accidently released these "weeds" to habitats where they should not be. The algae did not invade on their own, they were released into or transported to new environments by people. People created the problems, thus we must remember the mantra "Algae good; people bad." If you want to be a bit more kind toward people, you can use "Algae good; people iffy" as does one of my colleagues.

Red algae (Rhodophyta) There are ca. 4,000–5,000 species of red algae and, in striking contrast to the green algae, 90% of red algae are marine. Although there are some unicellular red algae, most are macroscopic algae often growing abundantly on rocky shores. Some molecular studies have indicated that the red algae are in the same monophyletic (natural) group as the land plants and the green algae, so one can argue that the red algae are real plants (although our working definition makes all of the algae "plants"). Some red algae are coralline and make calcium carbonate structures that are often very important components of "coral reefs" and in fact may be the major component in some reefs (the latter might be better called "biological reefs"). The red algae are the source of agar and carrageenans (sulfated polysaccharides used in hundreds of products including ice creams, beer, pâtés, shampoo, soy milk, and pet foods *inter alia*), and thus are harvested for commercial purposes. The red alga *Porphya* is also harvested as Nori and is the dark purple–reddish wrapper used in sushi around the world. The red algae are among the most beautiful seaweeds and many of them have been found to contain useful pharmaceutical compounds (with antibacterial, antiviral, or anti-cancer effects).

Brown algae (Phaeophyta) The brown algae can be thought of as the "macho algae" and include all of the giant kelps as well as smaller but equally "tough" intertidal seaweeds. There are only 1,500 to 2,000 or so species and they are almost entirely marine (even more so than the red algae). This group includes such famous entities as *Sargassum* of Sargasso Sea fame and the giant kelp *Macrocystis* which forms large forests and is harvested for alginic acid, a commercially important polysaccharide with a host of industrial uses from thickening food products to glossy paper production to beer brewing. Like the red algae, the browns are a source of potential pharmaceutical compounds. Like the greens and the reds, the brown algae are often major components of the rocky intertidal zone and thus are exposed at low tide and must withstand both desiccation and, in many cases, the full force of major wave action as the tides come in.

The small algae, the phytoplankton—the pasturage of the seas Although the seaweeds are often beautiful and often very noticeable (too noticeable when there are large blooms or when storms wash too much up on the beaches), they largely occur in coastal regions at or near the shoreline. In contrast the phytoplankton are microscopic and some are very beautiful. Although phytoplankton are often not noticeable at all (compared to the seaweeds), phytoplankton can be actually very noticeable when there is a massive bloom (such as the red tides and other Harmful Algal Blooms [HABs]). In such cases, the phytoplankton can change the color of the ocean for miles and poison the air. These algae are tiny, but the important thing to note is that the oceans and the major lakes of the world provide a vast habitat for the phytoplankton and they can achieve almost unimaginable densities. Indeed the vast number of phytoplankton cells are the initial food for marine and freshwater food webs (hence the expression "pasturage of the seas"). It is also the phytoplankton that generate most of the annual algal oxygen production (about half of the planet's total annual oxygen production). There are several interesting groups of marine and freshwater phytoplankton not covered in this brief introduction and there are important green algae phytoplankton—especially in freshwater ecosystems, but this review will stick to the marine Big 4 or Pasturage of the Seas, that is, the diatoms, dinoflagellates, coccolithophorids, and the blue–green algae.

Diatoms (Bacillariophyta)—algae in glass houses Microscopic, eukaryotic (nucleus-containing) diatoms literally make their wall (or "frustules") from silicon dioxide, that is, glass, and these glass walls overlap like the cover and bottom of a traditional lab Petri dish. Despite living in glass houses, the diatoms in some cases actually move around and at certain times even manage to have sex. But perhaps the single most important thing to note is that diatoms are often very abundant and, thus, important members of their respective ecosystems. The glass houses (or more scientifically, the frustules) survive for thousands of years and in fact diatomaceous earth (diatomite) used in pool filter systems and in car polishes is found in massive deposits sometimes hundreds of feet thick. There are 12,000 known species of diatoms and some estimate that there may be as many as 60,000 to 600,000 species (Hasle and Syvertsen 1997).

Dinoflagellates (Pyrrhophyta) The eukaryotic dinoflagellates are very abundant normally and can achieve densities of 10^7–10^8 cells per liter (Graham and Wilcox 2000) during blooms which are often HABs associated with paralytic shellfish poisoning, amnesic shellfish poisoning, diarrhetic shellfish poisoning, neurotoxic shelfish poisoning, and ciguatera fish poisoning. Given the litany of obnoxious poisoning that can be caused by dinoflagellates, one must return to the question: Are these algae bad? The answer is, of course, a resounding "No!" People bad; algae good. First, the dinoflagellates are mostly harmless sources of oxygen and food for other organisms. Second, whenever massive blooms of dinoflagellates occur there is most often a human cause, most typically excessive nutrients from anthropogenic pollution. Even if one notes that there are more HABs now than ever before and/or they are occurring in places where they have never occurred before and/or the blooms are worse in intensity than ever before, one must also note that human pollution is the cause of the blooms and the fact that they are occurring in new sites is undoubtedly due to human transport of dinoflagellates to new habitats (as, for example, via ship ballast water). So the problem, gentle reader, is not in our algae, but in ourselves. On a more positive note, dinoflagellates can exhibit bioluminescence and produce dreamlike scenes of people, boats, or dolphins moving through the water at night creating glowing trails. The dinoflagellates have a more serious role as the symbionts (or, zooxanthellae) of corals. Unfortunately increasing levels of pollution and increasing water temperatures cause "coral bleaching" wherein the algae abandon their coral hosts because of the unfavorable conditions and the corals die. A large percentage of the world's coral reefs are dead, dying, or threatened.

Coccolithophorids These eukaryotic phytoplankton species are fascinating in several ways. First there is their name: Coccolithophorids or "coccolith-bearers". What are the "coccoliths"? They are, often beautiful, calcium carbonate platelets borne on the surface of the flagellated unicellular algae. The exact function of the coccoliths is not understood, but there is experimental evidence that ocean acidification can clearly interfere with normal coccolith production and thus might have adverse effects on these important phytoplankton species. Another dramatic feature of the coccolithophorids is that they can be very abundant—so abundant in fact that they can turn the surface of the northern Atlantic whitish for miles and miles, and clearly can be seen in satellite photographs. The abundance of the coccolithophorids can be made dramatically clear when one considers that the flagellated unicells are microscopic—too small to be seen without a good microscope. And the calcium carbonate coccoliths that they bear on their surface are smaller still—each cell often bearing eight or more coccoliths as small as 1–3 μm in diameter. If one keeps in mind how tiny the coccoliths are and then considers the white cliffs of Dover and realizes that the chalk of the white cliffs of Dover is largely composed of coccoliths, one realizes that there had to have been billions and billions of coccolithophorids living and dying in the ocean over millions of years to generate such massive accumulations.

Blue–green algae (Cyanobacteria) It seems appropriate to return to, and conclude with, the prokaryotic blue–green algae, those hardworking photosynthesizers that changed the atmosphere of the planet. Like other prokaryotes the blue–green algae are abundant and present in almost every conceivable habitat from oceans and lakes (as expected), to ice, snow, thermal hot springs, and deserts (perhaps not as expected). Since more than 99% of all species ever evolved on Earth have gone extinct, it is probable that humans will (the optimist would say "might") be a relatively short-term component of life on Earth, but the blue–green algae that were major players 3.5 billion years ago at the start of life as we know it, likely will survive well after the large-brained, walking, talking animals have gone extinct. But while we and the blue–greens co-inhabit the planet, we owe them our thanks not only for the oxygen they produce and the vital role they play as primary producers in the food webs, but also for nitrogen fixation. Our atmosphere is filled with nitrogen and this inert gas prevents the oxygen in our atmosphere from igniting when we strike a match (when the first nuclear bomb test was planned there could have been at least a bit of concern that the buffering effects of nitrogen would not suffice and the whole planet might have gone up in flame but luckily that was not the case!). Living organisms must have nitrogen (hence millions of dollars spent on nitrogen-rich fertilizers around the world), but not in the form of the inert gas (two nitrogen atoms tightly bound by three covalent bonds). Thus, nitrogen fixation (or, the process of breaking those covalent bonds and adding other atoms like hydrogen and oxygen to the nitrogen) is, like photosynthesis and respiration, one of the most important physiological processes. The blue–green algae are nitrogen fixers which explains, in some cases, why blue–green algae can grow in such hostile environments and why we should thank the blue–green algae once again for what they do. Like the other phytoplankton algae described, the blue–greens are very abundant and can achieve bloom-level densities that color the water, often reddish (due to the red phycoerythrin pigment that can mask the blue–green phycocyanin pigment). Some suggest that Homer's "wine-dark sea" (or, "wine-faced sea") was "wine-dark" because of blooms of blue–green algae (specifically, *Trichodesmium erythraeum*). Of course, the question of how the blind poet Homer knew the sea was wine dark is an interesting question. (And, there are non-algal explanations for "wine-dark" as well, but they have no place in this introduction to the algae.)

But wait, there's more The algae changed the atmosphere of the planet, gave rise to the land plants, provide half of the planet's annual oxygen supply, are directly responsible for all seafood, and indirectly responsible for all "land food," and they help supply fixed nitrogen to support life on the planet. At this point our gratitude should know no bounds, but there is indeed still more. The major gas and oil deposits that we are so rapidly depleting came largely from Cretaceous algae deposits. Another thank you is in order. Various kinds of algae (but especially the blue–greens, reds, greens, and browns) are sources of new pharmaceutical compounds helpful in our battles against antibiotic-resistant bacterial strains plaguing our hospitals, against viral infections (including Herpes and AIDS), and against some forms of cancer. Another thank you... Lastly, we come to the latest potential major "gift" of the algae to humankind and one that will receive more attention in this journal issue, namely: the algae are a potential source of renewable biofuels—a source that from many perspectives is far more tractable than land plants (like corn or even sugar cane). In short, the algae are efficient harvesters of sunlight and do not waste much energy on intricate structure or pretty flowers. They can grow in brackish or salt water and do not need precious crop lands for growth. The algae can strip nutrients from polluted waters and they do use lots of CO_2 to grow and prosper. So, as we face the end of cheap fossil fuels and the perils of global warming, the algae might, once again, change things for the better and help give humankind some extra time before we go the way of 99.9% of all the species that have ever been. It would certainly be a grand advance if we found ourselves having to thank the algae yet again.

3 Conclusion

The algae have benefitted humankind since the earliest days of life on the planet—when the blue–green algae changed the planet's atmosphere and triggered the evolution of eukaryotic organisms including humans. They helped us again during the Cretaceous when our major current oil and gas deposits were generated by marine algae. They now provide about half of the planet's oxygen, a boon to those of us who breathe, and they directly or indirectly give us all of our food. The fact that the algae are also a potential source of renewable biofuels makes the world's most important "plants" even more important. Additional general information about the algae can be found in texts such as Algae (Graham and Wilcox 2000), Phycology (Lee 2008), and Algae—An Introduction to Phycology (van den Hoek et al. 2010). There are also many useful websites including but certainly not limited to the Phycological Society of America http://www.psaalgae.org/ and Michael Guiry's Seaweed Site http://www.seaweed.ie/guiry/.

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