# Aquatic Productivity under Multiple Stressors

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Aquatic ecosystems are responsible for about 50% of global productivity. They mitigate climate change by taking up a substantial fraction of anthropogenically emitted $CO_2$ and sink part of it into the deep ocean. Productivity is controlled by a number of environmental factors, such as water temperature, ocean acidification, nutrient availability, deoxygenation and exposure to solar UV radiation. These factors may interact to yield additive, synergistic or antagonistic effects. While ocean warming and deoxygenation are supposed to affect mitochondrial respiration oppositely, they can act synergistically to influence the migration of plankton and $N_2$-fixation of diazotrophs. Ocean acidification, along with elevated $pCO_2$, exhibits controversial effects on marine primary producers, resulting in negative impacts under high light and limited availability of nutrients. However, the acidic stress has been shown to exacerbate viral attacks on microalgae and to act synergistically with UV radiation to reduce the calcification of algal calcifiers. Elevated $pCO_2$ in surface oceans is known to downregulate the CCMs ($CO_2$ concentrating mechanisms) of phytoplankton, but deoxygenation is proposed to enhance CCMs by suppressing photorespiration. While most of the studies on climate-change drivers have been carried out under controlled conditions, field observations over long periods of time have been scarce. Mechanistic responses of phytoplankton to multiple drivers have been little documented due to the logistic difficulties to manipulate numerous replications for different treatments representative of the drivers.

aquatic ecosystems global climate change ocean acidification deoxygenation solar UV radiation

## 1. Introduction

The marine ecosystems cover 70.8% of our planet. Their primary productivity rivals that of all terrestrial ecosystems taken together [1], even though their standing crop is only about 1% of their counterparts on land [2][3]. The primary producers in these ecosystems include macroalgae, which are mainly confined to coastal habitats because they are sessile [4], with a few exceptions, such as members of the genus *Sargassum* which are found floating in the open ocean [5]. The highest concentration of marine biomass is found at higher latitudes and near the coasts. The majority of the aquatic primary producers consists of prokaryotic and eukaryotic phytoplankton both in freshwater and marine ecosystems [6][7].

Because of the requirement for solar radiation, the primary aquatic producers are restricted to the photic zone, the lower limit of which is defined as the depth where the light level has decreased to 1% of the surface irradiance [8]. This is the light level at which respiration compensates photosynthetic oxygen production. The physical depth of the photic zone depends on the concentrations of organic and inorganic dissolved and particulate matters, which are much higher in coastal than in oligotrophic open oceanic waters [9]. The prokaryotic and eukaryotic organisms form the basis of many extended food webs and sustain zooplankton, invertebrates, fish and mammals and provide food for the growing human population outcompeting the production of meat from terrestrial animals in many regions of the world [10].

The oceans absorb about 50–60 Petagram (PG) of anthropogenically released carbon per year. The biosphere in the oceans and on land absorbs about 45% of the anthropogenically released carbon dioxide [11]. The $CO_2$ concentration has increased from about 270 ppm before the industrial revolution to about 420 ppm today [12]. During the period from 2009 to 2018 the oceanic sink for anthropogenic carbon was about 2.5 ± 0.6 PG C per year, which drastically reduces the effects of global warming [11]. Part of the absorbed atmospheric $CO_2$ is taken up by phytoplankton in the top layer (photic zone) of the water column and sediments to the deep sea when the organisms die or in the form of fecal pellets as marine snow, a process called marine biological $CO_2$ pump [13][14].

## 2. Global Climate Change

Increasing anthropogenic emissions of greenhouse gases result in rising temperatures in the Earth's atmosphere, though the oceans have absorbed more than 90% of the Earth's back heating. Since 1979, the mean global air temperature has increased by 0.27 °C per decade [15], and the latest (6th) IPCC report predicts that limiting global warming to 1.5 °C will require drastic measures [16]. In contrast, the sea surface temperature increased at about 0.13 °C per decade due to the large buffering capacity of the oceans [17]. However, the increment is far from being uniform on the planet [18]. This is especially evident in the Arctic, where temperatures rise much faster than in most other parts of the world. This is in part due to a feedback mechanism: Ice and snow scatter and reflect the incoming solar radiation to a high degree [19]. As the ice melts, the open soil and water absorb solar radiation more strongly, heating the land and sea. As a consequence, the summer ice extent in the Arctic Ocean has decreased by about 45% during the last three decades [20][21]. This has dramatic consequences for the water column. The ice and snow cover protected the underlying photic zone from impinging solar UV-B radiation [22]. In contrast, the higher temperatures and increased impact of visible radiation supports a fast growth of phytoplankton in the upper layer which fosters an increase in consumer biomass [23]. Rapid ice melting reduces the salinity of the water and increases the amount of dissolved and particulate matter [24], which affects growth and species composition of the phytoplankton communities.

All organisms have specific thermal windows concerning their tolerance of thermal stress. We can define a lower limit, an optimum temperature and an upper limit. Tropical and subtropical corals have been found to die due to extensive heat that exceeds their permissive upper temperature limit [25][26]. Extended exposure to elevated temperatures results in the expulsion of their symbiotic zooxanthellae, which are photosynthetic dinoflagellates [27][28], resulting in massive bleaching and causes starvation [29][30]. The first signs of thermally induced damage can be detected by pulse-amplitude-modulated (PAM) chlorophyll fluorescence and photorespirometry. Exposure of *Stylophora pistillata* to 34 °C for 4 h resulted in a strong non-photochemical quenching, which indicates that the absorbed solar energy is no longer available to drive photosynthesis but is dissipated as heat [29]. Furthermore, the photosynthetic oxygen production and the quantum yield were drastically reduced. Bleaching is further aggravated by exposure to solar UV radiation especially at lower depths [31], as found in the sensitive *Pocillopora meandrina* up to a depth of 20 m, even though corals utilize a UV-absorbing pigment to protect them from UV radiation [32].

The temperature in the Mediterranean Sea is rising three times faster than in the global oceans [33]. Typical seagrasses and macroalgae in the area, such as *Posidonia oceanica*, *Cystoseira compressa, Padina pavonica*, *Caulerpa prolifera* and *Halimeda tuna*, differ in their thermal optima, and their upper lethal limits were found between 28.9 and >34 °C. The highest temperature optimum in this study was detected in *Cymodocea nodosa*. These results indicate that some species will profit from climate-change-induced higher temperatures by outcompeting other species, though little has been documented on their juvenile or spore/gamete stages. Increasing temperatures also change the species composition in phytoplankton assemblages [34], as indicated by comparing several thousand foraminifera communities from pre-industrial times with modern ones. Some species have been found to show a fast adaptation to increasing temperatures. Four diatom species isolated from the tropical Red Sea adapted to 30 °C after 200–600 generations and showed increased optimal growth temperature and their upper tolerated temperature limit [35].

Another option to deal with increasing temperature is a poleward migration [36]. In sessile organisms such as macroalgae and corals, it is a multigenerational process, while in motile forms, this can be achieved on shorter timescales [37]. For example, tropical and subtropical radiolaria have been found to move poleward, and this was especially pronounced during El Niño events [38][39]. The same effect was found in fish, such as cod, which migrate poleward to avoid heat stress and follow their food [40].

Increasing water temperatures result in higher stratification both in the ocean and in freshwater ecosystems [41], resulting in a defined upper mixed layer (UML) in which warmer and thus lighter water is vertically moved by winds and waves. The UML is typically 20 to 100 m deep in the oceans but much shallower in lakes on the order of a few to tens of meters, being shallower during summer seasons. The lower boundary of the UML is the thermocline, which every diver knows when he/she leaves the warm layer and dives down into distinctly colder waters [42]. The thermocline also limits the transport of nutrients-rich deep water up to the UML [43]. Most of the primary producers dwell in the UML, where they receive sufficient amounts of photosynthetically active radiation [44].

## 3. Ocean Acidification and its Effects

Along with the increasing $CO_2$ concentration in the atmosphere, the oceans quickly take up the anthropogenically released $CO_2$, with an approximate rate of 1 million tons per h. Such dissolution of $CO_2$ has been detected down to about 1000 m in depth. Since the oceans have already absorbed more than 30% of the anthropogenically released $CO_2$ [45][46], the marine carbonate chemistry has been being altered, with increased $H^+$ and decreased $CO_3^{2-}$ ions, along with increased concentrations of bicarbonate and total dissolved inorganic carbon. It is known that the oceans have been acidified by over 30% since the industrial revolution, even though the seawater has a high buffering capacity [47][48]. Predictions for the year 2100 indicate an increase by 100–150% of $H^+$, corresponding to a pH drop by 0.3–0.4 units [49][50][51]. The rate of this alteration in the world oceans chemistry is unparalleled in the recent ca. 1 million years [52].

The availability of $CO_2$ is a bottleneck for photosynthesis. Thus, it had been assumed that rising $CO_2$ concentrations in the water could fertilize the oceans by augmenting photosynthetic productivity in phytoplankton and macroalgae [53]. This has also been found for several phytoplankton groups at moderate increases in carbon dioxide [54]. However, many photosynthetic organisms possess $CO_2$-concentrationg mechanisms (CCMs), allowing them to use the large $HCO_3^-$ pool in seawater [55]. For these primary producers, increased concentrations of carbon dioxide may not have a significant effect [55], while for those which lack the CCMs, it appears to be an advantage [56]. Even organisms with CCMs have an advantage of higher $CO_2$ concentrations since they can downregulate this energy-consuming process and can better thrive in low-light conditions.

Some Rhodophyta, such as *Jania*, *Ellisolandia* and *Corallina* [57][58], and Chlorophyta, including *Halimeda, Codium*, *Halicoryne* and *Acetabularia* [59], are characterized by incrustation of calcium carbonate in the cell wall. Moreover, the Phaeophyta of the genus *Padina* incorporate calcium carbonate in their thallus [60]. Ocean acidification impairs the process of calcification [61][62][63][64]. This loss in calcification can be compensated at higher metabolic costs, thus decreasing productivity and growth rate [65].

Many zoological taxa use calcium carbonate for incrustations and accrustations, protecting against predators. A meta-analysis showed that ocean acidification decreases coral calcification, but the degree of the decrease is still uncertain [66][67]. Corals might be capable of adapting to lower pH values since samples collected from a site with naturally lower pH showed a higher degree of calcification and growth rate than samples from a site with a higher pH value [68].

## 4. Ocean Deoxygenation and Its Effects

Dissolved $O_2$ (DO) levels in the oceans are decreasing due to progressive ocean warming, which is known as ocean deoxygenation. The global ocean has lost about 2% $O_2$ per decade since 1960 in terms of the total ocean inventory [69][70], and the surface ocean $O_2$ levels have been projected to drop to about 200 $\mu mol\ L^{-1}$ by the end of this century ($-5\ \mu mol\ kg^{-1}$ per decade) [70][71]. Ocean warming decreases the $O_2$ solubility, hindering ventilation to deeper layers [72]. Consequently, the oxygen-minimum zones have spread out horizontally and vertically, along with ocean deoxygenation [71][73][74].

It is known that reduced $O_2$ levels are harmful, and hypoxia is detrimental to most marine animals [75][76]. However, natural phytoplankton assemblages and the diatom *T. weissflogii* have been recently shown to benefit from reduced $O_2$ concentrations by enhancing CCMs and by increasing carbon fixation efficiency [77], though such stimulating effects were moderated by ocean acidification treatment. Nevertheless, even under the influence of ocean acidification, deoxygenation can accelerate phytoplankton photosynthesis, consequently “re-oxygenating” in illuminated waters, which thus may progressively alleviate the impacts of deoxygenation on animals.

Dead zones appear largely lifeless [74], but algae and phytoplankton can provide oxygen to hypoxic habitats, provided that sufficient solar radiation and nutrients are available and they are in their tolerated temperature window. In contrast, animals are dependent on the availability of dissolved oxygen in the water, with the exception of zoological taxa with photosynthetic symbionts, such as corals, sponges or tunicates [78]. However, even coral reefs are threatened by accelerating ocean deoxygenation [79]. Some species are better adapted to hypoxia than others, as shown in the tolerant sea urchin *Echinometra viridis* from the Caribbean, as compared to two other species from the Pacific coast [80]. Some micrometazoan invertebrates, such as nematodes, have been found to be metabolically active at $O_2$ concentrations below 1.8 µmol $L^{-1}$ [81]. Zooplanktonic resting stages use cytochrome c oxidase as a sensor for the oxygen concentration signaling to exit dormancy [81]. Dead zones are also found in rivers and lakes, where they threaten the development of fish eggs, such as those of the grass carp (*Ctenopharyngodon idella*) [82].

## 5. Effects of Solar UV Radiation

Short-wavelength solar radiation has many—mostly deleterious—effects on the aquatic biota. Today, radiation at wavelengths below 280 nm (UV-C) is quantitatively absorbed by oxygen and the ozone in the stratosphere and does not reach the Earth’s surface, but it was a decisive component during the evolution before photosynthetically produced oxygen accumulated in the atmosphere, and, as a consequence, ozone became present in the stratosphere [83]. UV-B (280–315 nm) is partially absorbed in the atmosphere, while UV-A (315–400 nm) reaches the Earth’s surface almost quantitatively [84]. The irradiance impinging on the Earth’s surface is controlled by the solar zenith angle, atmospheric ozone, clouds, aerosols, surface albedo and height above sea level.

In terrestrial ecosystems, solar irradiances are controlled by circadian and annual changes and modulated by clouds and precipitation, and they are modified by global climate change. In addition, irradiances in aquatic ecosystems are modified by the tidal rhythm [85] and strongly controlled by the transparency of the water. Part of the radiation is reflected before penetrating into the water in dependence of the solar zenith angle and the smoothness of the water surface. Inside the water column, the radiation is attenuated by particulate and dissolved inorganic and organic matter. The inorganic material consists of sand and silt, especially in freshwater and coastal habitats [86]. Bacteria, phytoplankton and zooplankton form the particulate organic material (POM), while dissolved organic material is derived from decaying organisms and terrestrial runoff. Climate change affects the timing and amount of input by terrestrial runoff. UV radiation, in turn, photobleaches the dissolved organic matter (DOM) and breaks it down so that it can be more easily taken up by microorganisms. A large portion of DOM consists of chromophoric dissolved organic matter (cDOM), which controls the UV transmission in surface waters [87]. In the open ocean, cDOM and pigments are derived from the decay of marine producers such as algae and phytoplankton [88]. The browning of surface waters in North American and European boreal lakes is due to atmospheric deposition and surface runoff [89]. UV-B radiation has been reported to decrease by 12 to 39% over the period 1961–2014 for three lakes in Eastern and Southwestern China, resulting from decreased transparency [90].

Excessive solar UV radiation damages proteins, lipids, biomembranes and other cellular organelles [91][92]. One of the main targets for short-wavelength radiation is the DNA [93]. The most common damage is the formation of cyclobutane pyrimidine dimers (CPD) [94][95]. Cells have the capability to repair these lesions by using the enzyme photolyase, which utilizes the energy of UV-A and blue-light photons to split the dimers [96]. If not repaired the lesions may lead to mutations and death. Since the splitting of dimers is based on an enzymatic process, higher temperatures augment the repair [97].

In cyanobacteria, UV radiation impairs motility and orientation [98][99] and bleaches photosynthetic pigments such as the phycobiliproteins [100]. In addition to enzymatic repair, cyanobacteria and many other phytoplankton have developed protective UV-absorbing pigments to mitigate UV-induced damage [101][102], including an array of small-molecular-weight pigments, mycosporine-like amino acids (MAAs) of which more than 20 have been isolated and characterized [103][104]. Animals are not capable of producing MAAs, since they lack the shikimate pathway [105].

Organism groups, species and even cultivars vary in their sensitivity to solar UV-B radiation [106]. Generally speaking, primary producers in coastal habitats are more sensitive than those in open ocean waters, but due to the lower transparency of these waters, they are exposed to lower irradiances of short wavelength radiation [107]. Among macroalgae, red seaweeds are very sensitive, and, consequently, many species are found at a greater depth [108], while many green macroalgae are more tolerant and are found higher up in the eulitoral and sometimes even above the water during low tide [7]. The differences in UV sensitivity between cultivars of the same species can be explained by adaptation, nutrient supply and differences in experimental setup.

## 6. Effects of Multiple Drivers

Solar UV radiation (UVR, 280–400 nm) can damage DNA [91][92] and repress its repair in phytoplankton [109]. While UV-B irradiance represents less than 1% of the total solar energy, it is commonly more harmful than UV-A, as UV-B photons are more energetic than those of UV-A, which is about 6–8% of the total solar energy in subtropical areas. In addition, UVR can also generate active free oxygen radicals that lead to oxidative stress [91], lowering photosynthetic rates [110]. However, UVR, especially UV-A, may enhance photosynthesis of phytoplankton assemblages [111] and macroalgae [112][113]. Through historical adaptation, phytoplankton and macroalgae are able to cope with UVR, mainly by synthesizing UV-screening pigments such as MAAs and by eliminating active oxygen free radicals and repairing damaged proteins and DNA [91].

Ocean warming and acidification expose phytoplankton cells to higher temperatures and lower pH. The diatom *Skeletonema costatum* has been reported to increase the activity of periplasmic carbonic anhydrase (CAe) when exposed to moderate UVR levels and to raise its CCMs efficiency [114][115]. For the red tide alga *Phaeocystis globosa* grown under OA at 1000 µatm $pCO_2$ and full spectrum solar radiation with UVR, its photosynthetic efficiency showed the lowest values at noon [116].

Warming is suggested to alleviate UV-related damage due to increased activities of enzymes involved in repair processes [117][118]. When the diatom *Phaeodactylum tricornutum* had acclimated to two $CO_2$ concentrations (390 and 1000 μatm) for more than 20 generations, OA treatment enhanced the non-photochemical quenching (NPQ) of the cells and partially counteracted the damage of UVR to PSII, which, however, was moderated by warming treatment [119].

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