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## Productivity of aquatic primary producers under global climate change

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The productivity of aquatic primary producers depends on a number of biotic and abiotic factors, such as pH, CO<sub>2</sub> concentration, temperature, nutrient availability, solar UV and PAR irradiances, mixing frequency as well as herbivore pressure and the presence of viruses, among others. The effects of these factors, within a climate change context, may be additive, synergistic or antagonistic. Since some of them, e.g. solar radiation and temperature, vary along a latitudinal gradient, this perspective about the effects of global climate change on primary producers will consider ecosystems individually, separated into polar (Arctic and Antarctic), temperate and tropical waters. As coastal waters are characterized by lower light penetration and higher DOM and nutrient concentrations, they are considered in a separate section. Freshwater systems are also governed by different conditions and therefore also treated in their own section. Overall, we show that although there are general common trends of changes in variables associated with global change (e.g. the impact of UVR on photosynthesis tends to decrease with increasing temperature and nutrient input), the responses of aquatic primary producers have great variability in the different ecosystems across latitudes. This is mainly due to direct or indirect effects associated with physico-chemical changes that occur within water bodies. Therefore we stress the need for regional predictions on the responses of primary producers to climate change as it is not warranted to extrapolate from one system to another.

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## Introduction

More than 70% of our planet is covered by water, but less than 1% of this is freshwater.<sup>1</sup> The overwhelming share constitutes the vast marine ecosystems. In addition to their role in regulat-

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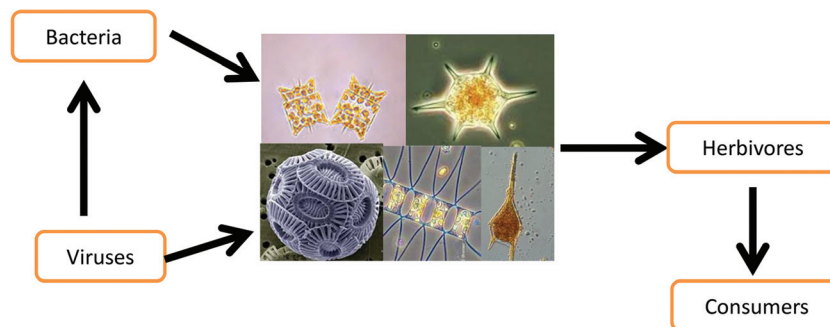
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**Fig. 1** Interconnections between bacterio- and virioplankton with phytoplankton as well as the input from the primary biomass producers to primary and secondary consumers.

ing the global climate by sequestering atmospheric CO<sub>2</sub>, marine ecosystems are major producers of human food sources including fish, crustaceans, mollusks and others.<sup>2,3</sup> During the last 50 years, world fish production has increased faster than global population growth, and today fish is an important source of animal protein for much of the human population.<sup>4</sup> Recreation and tourism is another significant aspect of marine ecosystems. For example, coral reefs have been estimated to generate an annual benefit of 9.6 billion US\$.<sup>5,6</sup> The basis of the marine food web is constituted by primary producers (Fig. 1), *i.e.* mainly phytoplankton, cyanobacteria and macroalgae that are the food source for primary and secondary consumers.<sup>7,8</sup> Even though the biomass (standing crop) of these marine organisms equals only about 1% of all plants in all terrestrial ecosystems, their productivity rivals that of the combined biomass production on land.<sup>9</sup> Other organisms have great significance in aquatic habitats, for example viruses are the most abundant biological particles in the sea<sup>10</sup> and especially viruses<sup>11</sup> play important roles in the structure and dynamics of aquatic ecosystems such as controlling phytoplankton populations.<sup>12</sup> Bacteria also have a key role in the microbial loop and carbon fluxes in the oceans.<sup>13</sup>

The marine ecosystems are a major sink for atmospheric carbon dioxide and take up a similar amount of CO<sub>2</sub> as all

terrestrial plants together and thus are a major player in the regulation of the atmospheric CO<sub>2</sub> concentration.<sup>14a</sup> While the CO<sub>2</sub> concentration in the atmosphere was estimated to be about 270 ppm before the industrial revolution it has currently increased to about 400 ppm.<sup>14b</sup> Without the constant uptake of CO<sub>2</sub> by the marine primary producers this value would be higher since about 25% of the carbon fixed in the upper oceans sinks to the deep sea<sup>15</sup> when the microorganisms decay or are eaten by primary and secondary consumers in the form of fecal pellets<sup>16</sup> in a process known as the biological pump. The increasing CO<sub>2</sub> concentration in the atmosphere might augment the growth and photosynthesis of phytoplankton.<sup>17,18</sup> However, at the same time it causes acidification of the water<sup>19,20</sup> and this anthropogenic impact on the ecosystem could be a threat for phytoplankton.<sup>21</sup> Additionally, the increasing CO<sub>2</sub> concentration,<sup>22</sup> which affects the CO<sub>2</sub> availability to the phytoplankton and also decreases the pH of the surface water, affects enzymatic and other biochemical processes as well as calcification in phytoplankton, macroalgae and animals with aragonite or calcite exo- or endoskeletons.<sup>23–26</sup> On the other hand, high concentrations of phytoplankton may be a partial solution to acidification, because the organisms take up the CO<sub>2</sub> during their photosynthetic activity.<sup>27</sup>

Primary productivity of marine organisms depends on a number of abiotic factors, with solar radiation being an essential environmental variable driving photosynthesis. Primary producers populate the euphotic zone, often defined as the water column between the surface and a depth where the surface irradiance has decreased to 1%, which allows positive net daily photosynthesis.<sup>28</sup> Terrestrial plants, as well as macroalgae, seagrasses, *etc.* attached to the bottom of an aquatic system, are confined to a habitat with a defined light level: in contrast, phytoplankton has to adapt to a wide range of irradiances within short periods of time as it is subject to constant movement within the mixing layer due to the action of wind and waves.<sup>29</sup> This passive movement is often superimposed by active vertical migration using flagella or changing their buoyancy.<sup>30</sup>

In addition to changes in the photosynthetic active radiation (PAR, 400–700 nm) these organisms are exposed to



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variable levels of UV radiation (280–400 nm) which can have detrimental effects on various morphological, physiological and genetic processes in the cells.<sup>2</sup> The severity of the effects caused by UV radiation varies with the taxonomic group, habitat and developmental stage, and planktonic organisms are affected to a larger degree than other groups.<sup>31</sup> In particular, effects such as reduction in primary production/ photosynthesis rates, growth, calcification and disruptions in membranes have been determined.<sup>32</sup> Since shorter wavelengths are more attenuated than longer ones due to Rayleigh scattering, UV-A (315–400 nm) can be more detrimental than UV-B (280–315 nm) radiation, even though the latter has higher damaging potential;<sup>33</sup> particularly UV-B is responsible for damaging the DNA molecule, *via* the production of cyclobutane pyrimidine dimers (CPDs).<sup>34,35</sup> However, there are variable responses, not only due to a high degree of species-specificity, but also due to the previous light history, for example when comparing phytoplankton of similar taxa (several chlorophytes and diatoms) isolated from tropical, temperate and Antarctic habitats, by exposing them to increasing doses of UV-A and UV-B, significant differences were found.<sup>36</sup> UV-A did not have an effect even at the highest doses applied, but UV-B inhibited growth. Thus the sensitivity depended on the species and on the biogeographic origin. Out of nine species, the Antarctic *Chlorella* was the least sensitive. Bacteria and viruses were found to be more affected by UV radiation than phytoplankton due to the fact that small cells cannot protect themselves from excessive short-wavelength radiation with reasonable concentrations of photoprotective compounds due to size restrictions.<sup>37</sup> This was confirmed for viroplankton in a transplant experiment simulating different latitudes. However viruses can adapt through evolutionary processes to different environmental conditions, such as UV radiation exposure.<sup>38</sup> In general, little is known about the effects of changing climate parameters on the viroplankton populations and virus–phytoplankton interactions.<sup>39</sup> While viruses are prone to be affected by UVR *via* radiation-induced DNA damage, they may obtain some protection from their hosts.<sup>40</sup> In bacteria, it was found that UV radiation exposure results in significant changes in the species composition of the communities.<sup>41</sup>

Detrimental effects of solar radiation on primary producers can be minimized by a number of mechanisms, among which the repair of damage, and synthesis of UV-absorbing compounds (mainly mycosporine-like amino acids, MAAs) are the most frequently found. Animals are not capable of MAA synthesis, but they take up these UV-absorbing substances with their food and use them for the same purpose by storing them in their outer cell layers.<sup>42</sup> In addition to their function as UV-absorbing pigments, MAAs were found to serve as antioxidant molecules scavenging toxic oxygen radicals.<sup>43</sup> Phytoplankton also uses other protective mechanisms to scavenge UV-induced oxidants, *e.g.* superoxide dismutase, ascorbate peroxidase and glutathione.<sup>44,45</sup> Also vertical mixing is essential in mitigating UV-induced photoinhibition as it allows the phytoplankton to repair damage to cellular compartments such as

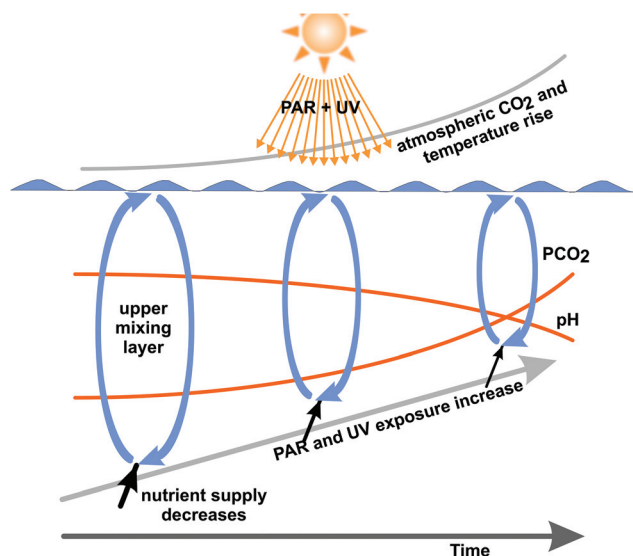
the DNA and the photosynthetic apparatus while being at the bottom of the mixing layer and therefore less exposed to intense solar UV.<sup>46</sup> Additionally, many terrestrial and aquatic animals as well as some higher plants are known to show compensatory growth after periods of reduced growth due to stress such as UV radiation exposure or darkness. Recently it was confirmed that this phenomenon also exists in the marine diatom *Phaeodactylum tricornutum* after being exposed to UV radiation.<sup>47,48</sup>

The ambient water temperature is another important external factor governing cellular productivity<sup>49</sup> since most biochemical processes are temperature-dependent. Only a few organisms can achieve net growth below freezing, and increasing temperatures result in higher productivity rates *via* a species-specific optimum up to a maximal permissive temperature.<sup>50</sup> Different taxa of primary producers have different abilities to acclimate to changing growth conditions such as temperature<sup>51</sup> which would result in different responses<sup>52</sup> including changes in the species composition with extensive consequences for the whole marine food webs. Increasing temperatures also support the occurrence of harmful algal blooms, many of which belong to the dinoflagellates.

Fossil records of dinoflagellate cysts indicate that El Niño events and changes in the North Atlantic Oscillation affect the population density of these phytoplankton groups by altering surface stratification, ocean currents and accessibility of nutrients.<sup>53</sup> Even when the supply of inorganic nitrogen is limited, blooms of toxic algae can develop, fed by a large pool of dissolved organic nitrogen (DON).<sup>54</sup> Another source of nitrogen can be submarine groundwater discharge.<sup>55</sup> In contrast, nitrogen limitation results in reduced biomass production and decreased synthesis of biogenic sulfur compounds such as DMS, DMSP and DMSO.<sup>56</sup> Phosphate limitation causes reduced alkaline phosphatase activity in phytoplankton and bacteria.<sup>57</sup>

Further environmental factors affecting the productivity of marine ecosystems are salinity,<sup>58</sup> pH,<sup>59</sup> nutrient availability,<sup>60</sup> competition between producers<sup>61</sup> and herbivore pressure.<sup>62</sup> Most of these factors are subject to marked changes caused by climate changes such as increasing temperature, ocean acidification, changes in nutrient availability due to changing oceanic streaming patterns and terrestrial runoff<sup>62,63</sup> as well as increasing exposure to detrimental solar UV-B radiation due to stratospheric ozone depletion.<sup>64</sup>

Even though the external factors such as temperature, pH, CO<sub>2</sub> supply, PAR and UV irradiances and mixing depths are known to be primary variables driving photosynthesis and production (Fig. 2), their interactions have received relatively little attention for both plankton<sup>65</sup> and sessile organisms.<sup>66</sup> This interacting web can only be disentangled by multifactorial analysis.<sup>67–69</sup> In addition, most studies have been carried out under laboratory-controlled conditions in short-term experiments.<sup>70,71</sup> In order to reveal the effects in real nature with its fast changing temperature, solar radiation and availability of nutrients, further studies need to be carried out in the open ocean with ecologically relevant values for the essential para-



**Fig. 2** Environmental factors due to anthropogenic activities, including atmospheric CO<sub>2</sub>, ocean acidification, temperature increase with reduction of the upper mixing layer and resulting increased exposure to solar UV and PAR are expected to be responsible for changes in future phytoplankton communities and marine primary production (adapted from ref. 22).

meters.<sup>22,72</sup> However, this is difficult and time-consuming regarding the vast areas to be covered and the low concentrations of cells in the water column. In order to evaluate the effectiveness of physiological and genetic adaptation to the changing growth conditions under a climate change scenario induced by anthropogenic activities, long-term studies together with multi-generation experiments need to be devised to understand how phytoplankton will cope with the various stress factors and take advantage of favorable conditions.<sup>73</sup>

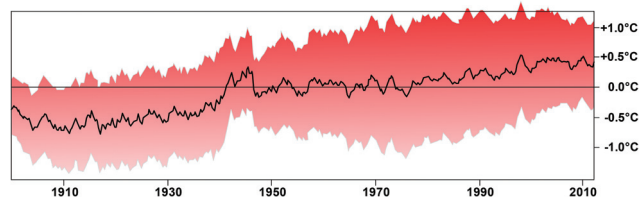
The impact of increasing temperatures on phytoplankton communities due to anthropogenically induced climate change is fairly well understood<sup>74</sup> and trends in abundance and shifts in the taxonomic composition are documented. However, the complex network of feedback loops,<sup>75</sup> changes in ocean chemistry and circulation patterns as well as the impact of tropical storms<sup>76,77</sup> need to be investigated since they will affect productivity and population dynamics with significant consequences for fisheries and climate development.<sup>78,79</sup> Many of the phytoplankton may not be impacted by the increase of CO<sub>2</sub> alone, but others, such as the ecologically important coccolithophorids, show a significant stimulation in growth.<sup>80</sup> Simultaneous increases in temperature and CO<sub>2</sub> in conjunction with increased UV radiation and nutrient limitations<sup>81</sup> were found to result in increasing cell sizes and elemental stoichiometry which are reliable predictors for tracking changes in the phytoplankton community structure and trophic dynamics.<sup>82</sup> Similarly, the inhibition of phytoplankton photosynthesis/growth by UV radiation cannot be seen as an isolated phenomenon as other factors such as temperature and grazer pressure play important additive, synergistic or mitigating roles in phytoplankton dynamics.<sup>83</sup>

Moreover, the effects of many feedback mechanisms on marine primary producers are largely unknown. Do higher temperatures of the oceans result in denser cloud covers? This could result in lower exposure of the phytoplankton to solar UV and PAR. Many phytoplankton and macroalgae are known to produce dimethylsulfoniopropionate (DMSP),<sup>84</sup> an organosulfur compound (CH<sub>3</sub>)<sub>2</sub>S<sup>+</sup>CH<sub>2</sub>CH<sub>2</sub>COO<sup>-</sup> that acts as an osmolyte or as an antioxidant.<sup>85</sup> This zwitterionic metabolite is excreted and partially broken down to dimethylsulfide (DMS, CH<sub>3</sub>SCH<sub>3</sub>).<sup>86,87</sup> DMS enters the atmosphere where it reduces the incoming solar radiation and forms cloud nuclei.<sup>88,89</sup> DMSP production and DMS release are correlated with sea ice melting.<sup>90</sup> The environmental advantage of DMSP-producing phytoplankton due to increased temperature could further complicate the feedback mechanisms involving cloud formation. Another expected climate feedback implication is the effect of nitrogen limitation on phytoplanktonic DMSP production and DMS release.<sup>91</sup>

As gradients of the most important factors affecting the primary productivity, *i.e.* radiation and temperature, occur in a latitudinal sense, we choose to organize this perspective considering such gradients starting with polar (both Arctic and Antarctic) waters, and then continuing with temperate and tropical communities. Since coastal habitats differ from open ocean ecosystems in a number of environmental factors they are considered in a separate section. The final section covers freshwater ecosystems.

## Phytoplankton in the Arctic Ocean

The Arctic Ocean covers an almost circular basin with about 14 million square kilometers surrounded by the Asian, European and American continents, with a small gap connecting to the Pacific Ocean *via* the Bering Strait, and another connection to the North Atlantic, with 45% of this area covered by permanent ice.<sup>92</sup> Increasing temperatures due to global warming, however, have decreased the ice cap dramatically over the last few decades by 49% during the summer as compared to the average area between 1979 and 2000.<sup>93–96</sup> The ice sheet also became much thinner and the total volume of ice in 2012 was only about 25% of that in 1979.<sup>97</sup> The temperature increase of the global oceans was about 1 °C over the last 112 years (Fig. 3).<sup>98</sup> The rise in Arctic near-surface air temperatures has



**Fig. 3** Global ocean surface temperatures (top 1 m) as compared to the average from 1900 to 2012 based on data compiled by Marinexplore (Sunnyvale, Calif). Redrawn from ref. 98. The gray area indicates the margin of error. The pronounced higher temperatures in the 1940s are an artifact due to the unavailability of data from Russia and Europe.

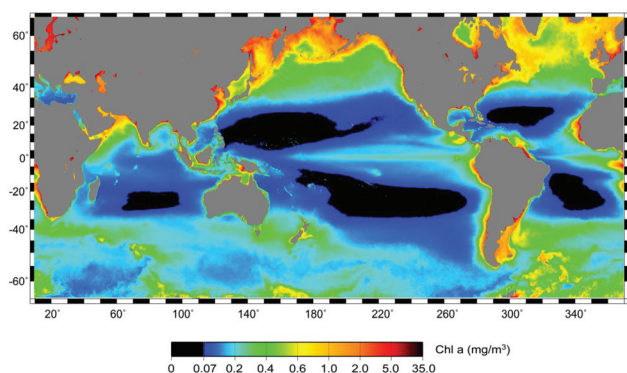


Fig. 4 Surface chlorophyll a derived from satellite measurements (NOAA [http://www.noaa.gov/news/stories/2008/20080305\\_ocean\\_desert.html](http://www.noaa.gov/news/stories/2008/20080305_ocean_desert.html)).

been almost twice as large as the global average in the past 2–3 decades.<sup>99</sup> This significant temperature increase is due to a feedback mechanism: while ice and snow reflect most of the incident solar radiation back into space, water and soil, which are no longer covered by ice, absorb most of this radiation causing a substantial warming.<sup>93</sup> As a consequence, summer melting occurs earlier and freezing later in the year and these not only produce a feedback effect in the recovery of the polar stratospheric ozone,<sup>100</sup> but also cause dramatic changes in the penetration of solar radiation in the water column.<sup>101</sup> The significant temperature increase augments the phytoplankton productivity and also affects the distribution of many plankton organisms. For example, tropical radiolaria have intruded into Arctic waters.<sup>96,102</sup> These plankton organisms were found in 2010 during a cruise northwest of Svalbard. Of the 145 taxa identified, 98 had probably been introduced with a pulse of warm Atlantic water which entered the Norwegian Sea and finally ended up in the Arctic Ocean. The tropical species even had different developmental stages indicating that they were reproducing here indicating increased ambient temperatures.

Phytoplankton concentrations are significantly higher in polar regions (both Arctic and Antarctic) than at mid or equatorial latitudes as seen from satellite imaging showing the chlorophyll fluorescence (Fig. 4).<sup>103</sup> The result of earlier melting and later freezing of the open water surface has prolonged the season for phytoplankton blooms<sup>27</sup> and also started about 50 days earlier than before.<sup>104</sup> Receding ice during the summer results in phytoplankton productivity further north, and this development attracts more fish. The Atlantic cod feeds on capelin, which used to have a maximal distribution south of Svalbard (75 °N) in 2000. In 2012 they had moved to 78 °N and the cod followed them.<sup>105</sup> Since the blooms are seeded from organisms entrapped in the ice over winter, the densest phytoplankton populations are found in the marginal ice zone within 100 km from the melting ice edge.<sup>106</sup> The peak of the blooms occurs within 20 days after the water has become ice-free. This is supported by strong storms which increase the concentration of nutrients in the photic zone. An evaluation of fluorescence data derived from

satellite measurements has shown a 20% increase in the net primary productivity in the open water of the Arctic Ocean between 1998 and 2009.<sup>107</sup> Usually nitrogen is limited in these waters, while phosphate and silicate are relatively abundant, but the melting sea ice contains about four times more nitrogen than the water.<sup>108</sup> These marginal sea-ice blooms have been confirmed for the Bering Sea, the Chukchi Sea and the Barents Sea.<sup>109–111</sup> Later in the growing season there may be a second bloom, when the water has heated up to support thermal stratification.<sup>112</sup> However, stratification also limits nutrient availability, since nutrient-rich bottom water is not easily mixed into the upper mixing layer (UML).<sup>113</sup>

Similar to phytoplankton in the water column, ice algae, that account for *ca.* 50% of the biomass in Arctic waters, also showed earlier growth than before, together with shifts in plankton species communities towards smaller cell types.<sup>27</sup> This selection of smaller phytoplankton types may be due to the low solar irradiances, which are more efficiently absorbed by small cells.<sup>114,115</sup> Recent studies carried out in the Chukchi Sea off the coast of Alaska in 2012 discovered an unprecedented giant plankton bloom under the Arctic ice shield.<sup>116,117</sup> The concentration of the phytoplankton was the highest ever recorded even in open waters. The blooms under the ice could not have been detected by remote sensing satellite-based fluorescence measurements. In some cases the blooms extended up to 50 m depth and more than 110 km from the edge under the ice. The melt water from the ice forms pools and puddles on the surface of the ice sheet which serve as “skylights”, where the light penetrates through the melt puddles almost unobstructed while the surrounding ice and snow are opaque.<sup>118a</sup> These pools focus sunlight through the ice and into the waters below. The penetrating light amounts to about 50% of the incident solar radiation,<sup>119</sup> allowing a massive growth of phytoplankton blooms underneath, further supported by nutrient-rich water under the ice.<sup>118a</sup> Under normal conditions polar sea ice transmits only a few percent of the incident solar radiation.<sup>118b</sup> If this phenomenon is more widespread in the Arctic Ocean, the phytoplankton would constitute a massive sink for atmospheric CO<sub>2</sub>. The thinner ice sheet, earlier melting and later freezing expose the phytoplankton to higher solar visible and UV radiation. This is partially offset by increased terrestrial runoff with high DOM content (dissolved organic matter) which reduces the transparency.<sup>120,121</sup> Melt water from sea ice and glaciers dilutes the sea water and reduces its salinity which may have far-reaching consequences for the food web since it changes the species composition and the abundance of phytoplankton.<sup>122</sup> Freshwater input in conjunction with the temperature increase enhances stratification shoaling the upper mixed layer and limiting the nutrient availability by reduced mixing between the UML and the water column underneath,<sup>123</sup> and this also favors smaller phytoplankton which has impacts on the food web *via* different food quality and size preferences of the food.<sup>124</sup>

Another factor damping the phytoplankton primary production in the Arctic is the reduction of solar radiation due to increasing cloudiness.<sup>125</sup> The presence of grazers may also

affect phytoplankton primary production.<sup>126</sup> However, grazers (<500  $\mu\text{m}$ ) did not affect significantly the phytoplankton productivity of bloom-forming communities (*i.e.* *Phaeocystis pouchetii*) as determined along a glacier-to-open sea transect in the Greenland subarctic fjord Godthåbfjord.<sup>127</sup> Visible light and UV radiation exposure also have important effects on the size structure of primary producers: picoplankton is more affected by solar radiation than nanoplankton, which could be explained by their smaller size, as shown in a mesocosm study in an Arctic fjord.<sup>128</sup> A similar change in phytoplankton communities due to UV pressure has been found in Arctic freshwater habitats.<sup>129</sup>

Additional anthropogenic stress factors are increasing environmental pollution. Especially in the Arctic shallow-water marine habitats, crude oil spills have been found to affect algae and bacteria. For example, pyrene, which is a component of crude oil in the sediment, has been found to exert a synergistic negative effect with increased solar UV-B radiation.<sup>130</sup> Phytoplankton has also been found to accumulate persistent organic pollutants (POP) in the Greenland Current and Arctic Ocean as documented during the ATOS-ARCTIC cruise.<sup>131</sup>

## Phytoplankton in the Southern Ocean (Antarctic)

In contrast to the Arctic, which is a closed basin, the Southern Ocean surrounding the continent is open to the Southern Pacific, the Southern Atlantic and the Southern Indian Ocean. The Antarctic continent is covered with ice and most of its coastline is hidden under ice flowing into the sea. Low temperatures are one factor for limiting photosynthesis and growth, but a more decisive one is light limitation.<sup>132,133</sup> Furthermore, phytoplankton growth in the Southern Ocean, away from the continental shelf, is limited by low concentrations of nutrients such as iron, nitrate and silicate.<sup>134,135</sup> In fact, iron and temperature have a synergistic effect on Antarctic phytoplankton and microzooplankton communities.<sup>136</sup> The major source of iron is from melting ice, Antarctic rocks and dust deposition.<sup>137,138</sup> In order to spur productivity, experiments have been conducted in which iron was sprayed onto the water.<sup>139</sup> This fertilization in fact resulted in a pronounced bloom of diatoms, taking up large amounts of  $\text{CO}_2$  from the atmosphere. However, these experiments are controversial, since further studies have indicated that the diatoms absorbed more iron into their silica shell than necessary for photosynthesis, depleting the Fe stock in the water.<sup>140</sup>

Antarctic shelf zones are generally very productive areas, and when the ice melts in spring nitrate, phosphate and silicate levels are high and allow vigorous growth.<sup>141,142</sup> As in the Arctic, in spring and early summer phytoplankton seeded from stocks frozen into the ice rapidly multiply forming a very dense population which covers thousands of square kilometers.<sup>143,144</sup> These dense blooms are several hundred times more concentrated than in mid-latitude oceans and provide food for primary consumers, mainly copepods,<sup>145</sup> krill<sup>146,147</sup>

and salps.<sup>148</sup> The amount of krill biomass has been estimated to exceed the weight of all human beings.<sup>149</sup> Ammonium and iron excretion from krill (*Euphausia superba*) is an important supply for phytoplankton.<sup>150</sup> The dominant phytoplankton species are *Phaeocystis antarctica* (in deeply mixed waters) and diatoms (in highly stratified waters).<sup>151</sup> Due to the high nutrient supply from upwelling water<sup>152</sup> and the long daylight hours biomass of phytoplankton and that of the following levels in the food web increase during the summer period. Physical gradients in the coastal waters and different stratified conditions are important external factors controlling the size structure and species composition in Antarctic phytoplankton.<sup>153,154</sup> Phytoplankton standing stocks and carbon assimilation rapidly increase during spring, reach a maximum in summer and decrease during autumn and are close to zero in winter.<sup>155,156</sup> During the winter in the Southern Atlantic the plankton is dominated by picoplankton (<2  $\mu\text{m}$ ) which represents 99% of the biomass. When the water temperature was below 1 °C mainly eukaryotes were found while above 1.3 °C cyanobacteria prevailed, such as *Synechococcus*. In contrast, *Prochlorococcus* was only found when the temperature exceeded 10 °C.<sup>157</sup>

Judging from 30 years of chlorophyll fluorescence data and field studies, densities of phytoplankton communities have dropped by 12% along the West side of the Antarctic Peninsula (Bellingshausen Sea) due to the rapid regional climate change.<sup>158</sup> The previously dry and cold climate became warmer and more humid, and it has long been observed that the Antarctic Peninsula is heating faster than any other part of the southern hemisphere. Winter temperatures on the Antarctic Peninsula have risen five times faster than the global average over the past 50 years, and are expected to do so in the future.<sup>159</sup> As a result, the sea ice cover has decreased dramatically allowing more wind mixing of the water column and more cloudiness, leading to decreased light levels and consequently less photosynthetic biomass production. In contrast, further south there are less mixing, fewer clouds and higher phytoplankton productivity.<sup>160</sup>

Heating of the water due to global warming has affected the base of the Antarctic food web. The accelerated warming resulted in a substantial loss of shelf ice and a significant input of freshwater into the sea. This dilution and reduction of salinity has far-reaching effects on the species composition of phytoplankton, bacteria and other components of the food web.<sup>161</sup> This was confirmed by the marked changes in phytoplankton composition during the onset of Antarctic glaciations in the early Oligocene (33.5 million years ago) as indicated by the fossil record of marine dinoflagellate cysts.<sup>162</sup> Predictions for the future posit a gradual loss of marine ice algae due to decreasing habitats as the sea ice disappears causing a cascade through the higher trophic levels of the food web; however, this is not regarded likely within the next 100 years. In contrast to the Arctic and the Antarctic Peninsula, the rest of the Antarctic continent has not experienced a marked warming.<sup>163</sup>

The Antarctic ecosystem is in a specific stress situation. Starting in the late 1970s a marked depletion of the

stratospheric ozone has been observed developing during spring.<sup>164</sup> This is due to specific chemical and physical conditions. Anthropogenically derived chlorofluorocarbons (CFC) and other trace gases accumulate in the stratosphere and are circled in a vortex over the Antarctic continent. These molecules trigger a catalytic destruction of ozone (O<sub>3</sub>) exceeding 50% loss.<sup>165</sup> Since O<sub>3</sub> is an effective absorber of solar UV-B radiation this energetic short-wavelength radiation reaching the water surface is dramatically increased. Even though UV-B radiation amounts to only about 1% of total solar radiation, it exerts damaging effects on different molecular targets in phytoplankton cells. Therefore a substantial increase in solar UV-B due to stratospheric ozone depletion can be assumed to have a marked effect on Antarctic phytoplankton primary production during ozone hole episodes.<sup>166,167</sup> Other studies have shown that UV radiation caused other effects such as reduction of growth, changes in the taxonomic composition in Antarctic phytoplankton<sup>168</sup> but these organisms have shown some capability to acclimate to solar UV radiation by the synthesis of ultraviolet-absorbing compounds.<sup>169,170</sup>

While a 25% of UV-afflicted inhibition of growth in the upper water column has been determined in Southern Ocean waters,<sup>171</sup> Smith *et al.*<sup>166</sup> calculated a 2% decrease for the annual primary production. *In situ* incubation of natural phytoplankton communities indicated that outside the ozone hole solar UV-B is responsible for about 4.9% inhibition of primary production, while under ozone hole conditions (150 Dobson Units) the inhibition rose to 8.7%.<sup>172</sup> In contrast, Hamre *et al.*<sup>173</sup> even found an enhanced aquatic primary production by 1% for 50% stratospheric ozone depletion. Antarctic coastal phytoplankton assemblages are generally much less sensitive to UV radiation than open ocean communities,<sup>174</sup> with also higher rates of repair than pelagic communities. Variable irradiance conditions, as experienced by phytoplankton in the UML, were of key importance at the time to determine the impact of solar UVR. Helbling *et al.*<sup>175</sup> determined that the combination of solar UVR and vertical mixing decreases the primary productivity of Antarctic phytoplankton. Later studies proposed a model showing that fast vertical mixing was more important than the low total column concentration in decreasing the primary productivity of phytoplankton in the Antarctic.<sup>176</sup> This was related to the low temperatures in the Southern Ocean and the low repair capacities as compared to other ecosystems. Increasing global temperatures would have an important effect on polar phytoplankton by increasing metabolic rates and thus repair mechanisms to cope with solar UVR.

## Phytoplankton from temperate ecosystems

In contrast to polar or tropical aquatic ecosystems, temperate environments undergo great changes in physical factors such as temperature, wind, *etc.*<sup>177,178</sup> At temperate latitudes phytoplankton communities present seasonal cycles of abundance

and species composition.<sup>179</sup> These are mainly driven by factors varying seasonally,<sup>179</sup> acting directly or indirectly, antagonistically, synergistically or additively.<sup>68</sup> These factors include temperature (which affects biochemical and enzymatic processes such as SOD activity,<sup>180</sup> and photosynthetic processes,<sup>181</sup> among other things), light availability<sup>182</sup> and the impact of excessive visible and UV solar radiation.<sup>183,184</sup> For example, as the temperature increases towards the summer, stratification tends to increase, decreasing the thickness of the UML.<sup>185</sup> In addition, many other external factors including water currents, pH,<sup>186</sup> DOM concentration,<sup>187</sup> salinity, mixing layer depth<sup>188</sup> and nutrient availability like nitrogen and iron<sup>189</sup> vary seasonally and affect phytoplankton development and abundance.<sup>190,191</sup> In temperate environments, however, wind is perhaps the most important factor controlling the stratification of the water column and together with this, the development of winter blooms which favored large diatoms, while pre- and post-bloom periods were characterized by small (<10 μm) flagellates, as seen in Patagonian waters.<sup>179,192</sup> Harmful red tide dinoflagellate blooms are also an important issue in temperate marine habitats, especially in coastal and estuarine ecosystems. These blooms have been found to increase with increasing nutrient availability, *e.g.* from terrestrial runoff. They are further enhanced by rising temperatures<sup>53,193</sup> and spread globally by being carried by marine transport in ballast water.<sup>194</sup>

Rising temperatures due to global climate change are expected to affect temperate phytoplankton most pronouncedly during winter and early spring while the effects will be much smaller during the rest of the growth season.<sup>191</sup> However, higher temperatures moderate the inhibition of carbon fixation and photochemical quantum yield, as shown for the cosmopolitan diatom *Thalassiosira weissflogii*.<sup>184,195</sup> One of the reasons for this is a significantly higher RUBISCO activity and gene expression of this enzyme at 25 °C than at 20 °C. Therefore, this mechanism could reduce the UV stress on phytoplankton in a global climate change scenario. In contrast, a mesocosm experiment in the Saint Lawrence Estuary indicated that higher temperatures impair the cell cycle resulting in lower growth rates and cell concentrations in natural phytoplankton communities.<sup>196</sup>

Changes in stratification and in the UML depth will affect not only phytoplankton production, by changing the exposure of cells to solar radiation, but also to higher trophic levels such as fish from temperate zones.<sup>178</sup> Under mixing conditions, UV-A can even have positive effects on growth, as it can be utilized for photosynthetic energy harvesting.<sup>197,198</sup> However, the extent of UV effects strongly depends on the phytoplankton community composition as shown for natural assemblages in a temperate estuarine ecosystem.<sup>199</sup> For example, cryptomonads were found to be significantly more sensitive to UV radiation than the common estuarine diatom *Thalassiosira*. Levels of MAAs have been found to increase with rising exposure to solar radiation. The occurrence of specific MAAs can be correlated with the advent of key phytoplankton species in the water column. For example, in the English

Channel the concentration of mycosporine–glycine was found to increase in parallel to the occurrence of a *Phaeocystis* bloom in spring.<sup>200</sup> Later in the year an unidentified MAA ( $\lambda_{\text{max}}$  328 nm) was found to match a bloom of the diatom *Guinardia striata*. The strong correlation between solar UV radiation and MAA concentration was proven by monitoring the daily variation in the cellular concentration of MAAs in the marine dinoflagellate *Scrippsiella* independent of cell volume or chlorophyll *a* concentration.<sup>201</sup>

The sensitivity to UV-B of temperate phytoplankton assemblages was found to be dependent on the nitrogen (and also phosphate and silicate) availability.<sup>202</sup> As long as sufficient nutrients were available within the mesocosms UV-B effects were minimal but the cells suffered from significant photo-damage to the PSII reaction center, monitored as a decrease in the D1 protein pool, when nutrient supply was limited.<sup>203</sup> Also, in a survey on carbon fixation of natural summer phytoplankton assemblages from Patagonia high photosynthetic efficiency was found favored by the input of inorganic nutrients from the Chubut River which discharges close to the site of plankton collection.<sup>204</sup> In natural phytoplankton communities the effects of solar UV-B on the photodegradation and repair of the PS II D1 protein were studied during a 5-year multidisciplinary project.<sup>205</sup> These studies showed that the inhibition of the repair cycle by UV-B is more important than the original damage of the protein. Biochemical analysis indicated that the phosphorus supply, irradiance and temperature affect the fatty acid concentration in chlorophytes, cryptophytes and diatoms.<sup>206</sup>

Large-celled diatoms have a higher capacity to withstand and exploit high light irradiances.<sup>207</sup> Small-celled phytoplankton such as the cyanobacterium *Prochlorococcus* and picoeukaryotes are more prone to UV-B-induced damage than larger cells.<sup>208–210</sup> This was confirmed by exposing Atlantic picophytoplankton communities to natural levels of solar radiation.<sup>210–213</sup> Even when using an experimental approach to simulate vertical mixing, solar UV radiation was found to affect microplanktonic diatom species (*Odontella aurita*) during the summer bloom and nanoplanktonic flagellates and *Chaetoceros* after the summer bloom in a temperate South Atlantic location (43 °S).<sup>197</sup> Further *in situ* experiments at the same area confirmed that solar radiation induced DNA damage and caused inhibition of photosynthesis in the top 3 to 6 m.<sup>214</sup>

The concentration of phytoplankton strongly depends on the pressure by predators. In a study on the seasonal abundance and feeding patterns of copepods in a pelagic food web in the White Sea up to 85% of the phytoplankton standing crop was consumed by the calanoid copepods, playing a significant role in the transformation of particulate organic matter.<sup>215</sup> As also seen in freshwater and tropical habitats, the extent of UV-B stress on phytoplankton affects the palatability of these cells during zooplankton grazing.<sup>216</sup> While *Daphnia* grazing was not affected by UV-B stress on *Chlamydomonas*, *Microcystis*, *Cryptomonas* and *Scenedesmus*, *Brachionus* grazing rates decreased.

## Tropical marine habitats

In contrast to temperate and polar areas, where the UML can exceed 100 m of depth, tropical aquatic systems tend to have a strongly stratified and stable mixed layer, driven by temperature, and typically restricted to the top 10–20 m.<sup>185</sup> This stability in physical–chemical factors is evidenced in the low variability in phytoplankton species composition in the tropics.<sup>217</sup> Most tropical waters are exceptionally clear, since the density of phyto- and zooplankton is very low due to limited nutrient supply in these oligotrophic waters. These low nutrient conditions favor growth of small-sized cells, and although numerous cruises confirmed a strong variability in phytoplankton chlorophyll concentrations in the Eastern North Atlantic Subtropical Gyral Province, they indicated that 54% of the primary production was contributed by cells <2  $\mu\text{m}$ .<sup>218</sup> Below the marked pycnocline nutrient concentrations are considerably higher and the irradiances are lower, resulting in a distinction of phytoplankton organisms populating the highly lit, but nutrient-deficient mixing layer and those in the zone below.<sup>219</sup> Tropical offshore habitats also have a low concentration of nutrients due to the lack of upwelling water. Some of the nutrients such as iron are derived from aerosols especially from desert regions as shown for oligotrophic North Atlantic and Caribbean waters.<sup>220</sup> Expected higher temperatures due to global climate change will even strengthen the pycnocline making transition in and out of the mixing layer more difficult.<sup>221</sup> In addition, temperatures are at the upper limit for many phytoplankton species, so that further increases due to global climate change may exceed the permissive thermal window for some organisms.

As a result of low concentrations of particulate and dissolved materials in the water column, penetration of high irradiances of both PAR and UV radiation reaches levels deep down into the water column. This was confirmed by a global ocean-atmosphere model which showed that the 10% penetration at various UV wavelengths was the highest in the oceanic gyres and the lowest in optically complex continental shelf regions.<sup>222</sup> In addition, in the tropics the solar zenith angle at noon is very low throughout the year, and thus tropical habitats have no marked seasonal changes with high PAR and UV irradiances year round.

As a consequence of high solar radiation levels, phytoplankton is under considerable radiation stress.<sup>223</sup> Also, measurements in a tropical lagoon in New Caledonia revealed that inhibition of phyto- and bacterioplankton increases with oligotrophy and that the deepest limit of UV inhibition of phytoplankton was at about 8 m depth.<sup>224</sup> On sunny days both small pico- and nanoplankton, but also larger microplankton, have been found to be strongly affected by solar UV radiation, mostly UV-B.<sup>225</sup> Carbon incorporation was inhibited throughout the summer, and during the peak growth period the phytoplankton assemblages were dominated by the diatom *Skeletonema*, while in the rest of the time the phytoplankton concentration was low (as estimated by chl *a* concentrations) and the samples mainly contained monads and flagellates.



In contrast, on cloudy days the microplankton (>20  $\mu\text{m}$ ) was found to utilize UV-A as an energy source for photosynthesis, while the pico- and nanoplankton were still inhibited by UV radiation.<sup>226</sup> In coccolithophorids UV-B strongly inhibited the photosynthetic apparatus, while longer wavelengths impaired the calcification process.<sup>227</sup> In *Emiliania huxleyi* decreased calcification resulted in a down-regulation of the photoprotective mechanism.<sup>71</sup> Also, elevated temperatures increased photosynthesis and calcification in this organism, in contrast exposure to elevated levels of UV radiation decreased the rates of photosynthesis and calcification.<sup>227</sup>

Excessive solar radiation induces mortality in tropical marine picoplankton in oligotrophic waters.<sup>211</sup> The cyanobacterium *Synechococcus* and eukaryotic phytoplankton were more resistant to solar UV and PAR than the picoplanktonic cyanobacterium *Prochlorococcus*. Total mortality was also significantly higher in all taxonomic groups when exposed to unfiltered solar radiation than to radiation with the UV-B component filtered out. Even short exposure of 30 min to tropical solar radiation induced mortality in *Prochlorococcus*. The mechanisms facilitating survival in some groups have not yet been determined.

Solar UV-B was found to affect natural phytoplankton assemblages in a subtropical marine bay in Southern China.<sup>209</sup> When quantifying the quantum yield it was found that exposure to solar UV-B decreased growth by 17–49% under unfiltered solar radiation as compared to 11–22% reduction under radiation deprived of UV-B. Even though the phytoplankton was mixed passively in the upper mixing layer, samples collected at 4 m depth were more sensitive to solar UV-B than surface samples. Clearly, exposing phytoplankton samples at a fixed depth, e.g. when they are confined in a quartz vessel, inhibits growth and photosynthesis more than under natural conditions, when the organisms are moved within the mixing layer.<sup>228</sup> Using simulated mixing during an experiment involving phytoplankton assemblages from the South China Sea confirmed that mixing of the cells within the water column largely reduced the UV-induced inhibition of photosynthesis which was dependent on the mixing frequency and the depth.<sup>229</sup>

Increasing temperatures due to global climate change may have additional effects on biomass production and species composition of tropical phytoplankton communities affecting higher levels in the trophic food web and increasing the vulnerability in the Barrier Reef ecosystems.<sup>230</sup> In experiments carried out with natural assemblages isolated from a reef lagoon in the Mexican Caribbean grown in microcosms under two natural radiation conditions (unfiltered vs. only PAR radiation)<sup>231</sup> it was found that at ambient temperature (28 °C) there was a shift from flagellates to diatoms during the 16 day incubation. At 3 °C higher temperature dinoflagellates and cryptophytes as well as the most frequent diatom *Cylindrotheca* decreased in density whereas small chlorophytes prospered and represented most of the biomass at the end of the exposure indicating that increasing temperatures will modify the species composition of natural phytoplankton communities exposed to natural solar radiation in tropical assem-

blages. There is evidence that shifts in species composition may also be induced by synergistic pollution (e.g. PAH) effects leading to higher densities of heterotrophs which will affect the carbon cycle in the ocean as well as changing the role of the ocean as a major sink for atmospheric CO<sub>2</sub>.<sup>232</sup>

## Coastal phytoplankton communities

Coastal habitats are characterized by higher concentrations of organic and inorganic particulate and dissolved materials, decreasing the penetration of solar radiation into the water column (Fig. 5). Specifically the concentrations of sediments<sup>233</sup> and UV-absorbing DOM are significantly higher,<sup>234</sup> exposing the phytoplankton to lower levels of detrimental UV-B than in open ocean habitats at comparative water depths.<sup>235,236</sup> Coastal phytoplankton (with the exception of Antarctic ecosystems) is commonly more sensitive to solar UV radiation than open ocean species.<sup>179</sup> This is due to the higher DOM concentrations and lower transparency so that the cells are “dark” acclimated and need less protection mechanisms<sup>237</sup> and, for example, they have lower MAA concentrations.<sup>238</sup> Still the levels of natural UV-B are detrimental in many coastal areas, partly because the phytoplankton is confined to a shallower mixing layer. Comparing photosynthetic carbon fixation in coastal and offshore surface waters in the South China Sea confirmed that the corresponding levels of solar UV-B caused similar inhibition (about 28% under clear skies), but UV-A effects increased with the distance from shore, about 4% for coastal waters vs. 13% for offshore waters, respectively.<sup>239</sup>

Usually coastal waters have higher nutrient concentrations due to both upwelling on the continental shelf and terrestrial runoff<sup>240</sup> and can thus accommodate higher phytoplankton growth.<sup>241</sup> Higher nutrient availability can also result in a different species composition from open oceanic waters as shown in an enclosure experiment with added N and P.<sup>242</sup>

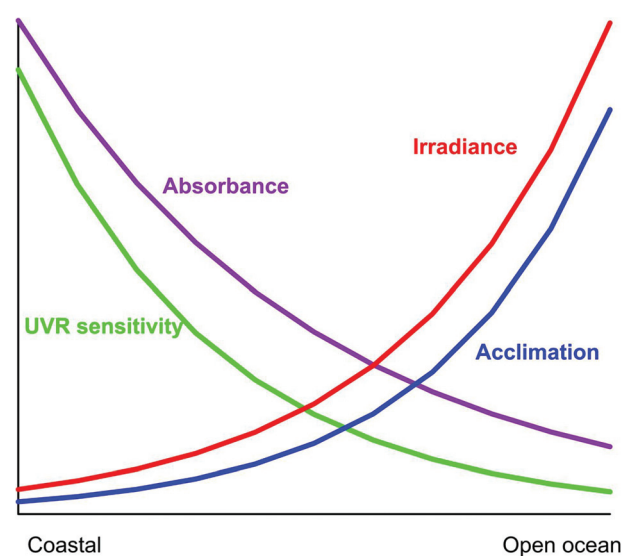


Fig. 5 Gradients of key environmental factors as a function of the distance from the coast to open waters.

High solar UV irradiances affect phosphorus cycling<sup>243</sup> and the uptake by phytoplankton as demonstrated with <sup>32</sup>P. Experiments carried out in a 13000-l mesocosm set up in an estuarine environment in Rhode Island showed that UV-B induced significant inhibition of phytoplankton above the thermocline but not below, indicating the significance of stratification within the water column.<sup>244</sup> A series of mesocosm experiments at three different latitudes (Canada, Brazil and Southern Argentina) using lamp-enhanced UV-B radiation, simulating 30% or 60% ozone depletion, respectively, showed pronounced changes in species composition of both phytoplankton and grazers (ciliates).<sup>245</sup> However, no significant decrease in algal biomass was detected which was attributed to the mixing inside the mesocosms. High nutrient concentrations in coastal waters often were responsible for blooms of toxic phytoplankton but these were found not to be affected by solar UV-B radiation in coastal waters of Japan.<sup>183</sup>

Coastal marine environments are also under the pressure of human influences.<sup>246</sup> Pollutants such as polycyclic aromatic hydrocarbons (PAH)<sup>247</sup> and water-soluble fractions of heavy oil also affect plankton communities.<sup>248</sup> When added to a mesocosm, bacterial growth accelerated quickly, but decreased two days later, corresponding to an increase in small heterotrophic flagellates and viruses. The oil fraction attached to diatoms, which in turn sedimented, so that the oil pollutant was removed from the water column by vertical sedimentation.<sup>249</sup> These aliphatic and aromatic hydrocarbons are also taken up by phytoplankton communities where they accumulate.<sup>250</sup> Another study investigated the synergistic and non-synergistic ecotoxicological effects of solar UV-B and organic pollutants, such as atrazine, tributyltin or crude oil<sup>251</sup> which enter coastal waters from terrestrial drainage or maritime traffic.<sup>251,252</sup> Natural phytoplankton communities pre-stressed with UV-B were more susceptible to the pollutants than those grown under UV-free conditions. The toxicity of PAH for oceanic phytoplankton is also enhanced by solar UV as shown with natural communities from the Mediterranean Sea, Atlantic, Arctic and Southern Ocean.<sup>253</sup> The PAH toxicity was confirmed for all phytoplankton groups, but only for the picoplankton the synergy was observed with UV radiation.

Coastal waters usually also harbor high bacterioplankton concentrations due to the availability of humic substances.<sup>254,255</sup> This was confirmed for a coastal upwelling system, where photodegradation of residual humic substances provided nutrients for bacterioplankton growth.<sup>256</sup> Even though they are under high pressure from UV-B and UV-A they recovered rapidly when the solar radiation decreased during the daily cycle.<sup>257–259</sup> In an *in situ* analysis the highest bacterioplankton activity was found between 5 and 10 m, where short-wavelength UV-B radiation was largely attenuated.

## Freshwater phytoplankton

One of the main differences between open oceans and freshwater ecosystems is the transparency to visible and UV

radiation. High concentrations of DOM and particulate organic material (POM) attenuate solar radiation within the top layer of freshwater environments,<sup>260</sup> making them similar to coastal systems. However, penetration of solar radiation also depends on the salinity of the water, *i.e.* UV radiation penetrates more deeply in saline prairie lakes than in freshwater habitats with the same concentration of DOC.<sup>261</sup> Using long-term data from five North Andean Patagonian lakes, Modenutti *et al.*<sup>262a</sup> showed that ashes from the Puyehue volcano eruption in 2011 resulted in 1.5- to 8-fold increases in total suspended solids, light extinction and phosphorus concentrations relative to pre-eruption conditions. While the light attenuation resulted in lower light availability, this was over-compensated by enhanced growth due to the increased nutrient input. The UV transparency in lakes undergoes pronounced seasonal variations; this is due to the timing of plant litter shedding in temperate zones, and storm events such as the case of Saharan dust over high mountain lakes in Sierra Nevada.<sup>262b</sup> But even above the tree line a change in transparency was found associated with changes in phytoplankton biomass.<sup>263</sup> While the transparency in the top 4 m of an alpine lake was fairly constant over time, it decreased in the lower zone (4–9 m depth) with time after the ice break due to increasing CDOM concentrations.<sup>264</sup> Other external factors such as temperature, nutrients, dissolved oxygen and pH also affect the seasonality of phytoplankton growth.<sup>265</sup> Also phytoplankton contributes to the concentration of biodegradable DOC as shown in diatom blooms in freshwater enclosures.<sup>266</sup> The high transparency of alpine lakes together with the natural increase in solar UV-B radiation with altitude<sup>267</sup> are the major factors affecting phytoplankton in these habitats.<sup>268</sup> In an attempt to predict future changes in Arctic and Subarctic small lakes due to global warming, models have been developed using environmental factors such as dissolved organic carbon (DOC) concentrations, weather and water acidification affecting the transparency and thus the development of organisms.<sup>269,270</sup>

Depending on the concentration of CDOM growth inhibition of phytoplankton by solar UV-B can vary between 2.5 and 26% as shown in a study by Harrison and Smith.<sup>271</sup> The exposure to low UV fluxes should reduce the risk of cellular damage in phytoplankton; but being adapted to lower levels of short-wavelength radiation and thus being more sensitive at least partially offset the protection by strong attenuation.<sup>7</sup> Hessen *et al.*<sup>62</sup> found an increase in phytoplankton growth in an Arctic lake when they artificially added DOC. However, this effect was soon canceled by the fast growth by more than 300% of the zooplankton predators which consisted almost exclusively of *Daphnia tenebrosa*. In other locations, with higher solar UV radiation, this factor may also affect the zooplankton, as shown in 53 lakes in Patagonia and Chile.<sup>272</sup> The input of allochthonous organic carbon from terrestrial runoff increases the growth rate of bacterioplankton which mineralizes the humic substances, thus providing higher nutrient concentrations for phytoplankton which affects the biomass productivity and community structure within both

the phyto- and zooplankton.<sup>273</sup> Different taxa of phytoplankton have different sensitivities to solar UV radiation as shown in incubation experiments with species from three Arctic lakes.<sup>129</sup> Small chlorophytes, diatoms and picocyanobacteria were more affected by UV-B than larger colony-forming cyanobacteria and chrysophytes. Therefore the latter dominated the assemblages at the end of the exposure. This was supported by the fact that the larger colony-forming species could not easily be consumed by daphnids. UV radiation can also stimulate the freshwater food webs as DOC is broken down into smaller fragments it causes an increase in bacterial abundance resulting in an increase in bacterivore populations which positively affects the subsequent trophic levels *via* the microbial loop.<sup>274</sup>

In order to harvest sufficient solar energy for photosynthesis, phytoplankton moves actively or passively higher in the water column. In addition, the mixing layer tends to be thinner in freshwater habitats than in oceanic waters therefore exposing the cells to high solar radiation.<sup>275</sup> When studying the combined impact of UV radiation, nutrient and vertical mixing over a series of lakes with different attenuations of solar radiation, Helbling *et al.*<sup>69</sup> demonstrated that vertical mixing under ambient nutrient conditions produced a synergistic effect with UV radiation, increasing phytoplankton photosynthetic inhibition and excretion of organic carbon from opaque lakes as compared to algae that received constant mean irradiance within the epilimnion. In clear lakes, however, these effects were antagonistic with mixing partially counteracting the negative effects of UV radiation. Addition of nutrients, mimicking atmospheric pulses from Saharan dust, reversed this general effect, suggesting an alteration in the microbial loop and trophic interactions due to enhancement of EOC.<sup>69</sup>

Growth inhibition of phytoplankton by UV radiation is further aggravated by the lack of phosphorus supply.<sup>276</sup> Because of differential sensitivities of species, simultaneous UV exposure and P limitation caused shifts in the species composition in boreal lake phytoplankton communities.<sup>277</sup> Mesocosm studies in a high-altitude Spanish lake have shown that addition of P increased the fatty acid content,  $\omega$ 3-polyunsaturated fatty acids and the chlorophyll *a* to carbon as well as the C to N ratios in seston.<sup>278</sup> UV radiation also increased the fatty acid content and  $\omega$ 3-polyunsaturated fatty acids, but reduced the C to P ratio in seston. These results show that the interaction between UV and P reduced the food quality of phytoplankton by reducing the content of highly unsaturated fatty acids for the next trophic level especially in oligotrophic habitats exposed to high solar UV. Exposure to solar UV-B also affects the quality of phytoplankton as food for zooplankton such as *Daphnia*.<sup>279</sup> Size at maturity was lower in organisms fed on UV-B-irradiated *Cryptomonas* but not on *Chlamydomonas*. Thus exposure of phytoplankton to UV-B affects the energy transfer from the first to the subsequent levels in the food web. However, another study showed that UV radiation affects photosynthesis and the pigment composition in periphyton but not the food quality.<sup>280</sup>

Solar UV-B damages cellular DNA in freshwater phytoplankton inducing mainly CPDs and, to a smaller extent, pyrimidine (6–4) pyrimidone photoproducts (6–4 PP) and their Dewar isomers.<sup>281</sup> Thymine dimers in three rice-field cyanobacteria (*Anabaena*, *Nostoc* and *Scytonema*) were quantified using blotting and the chemiluminescence method.<sup>282</sup> The frequency of thymine dimers increased with increasing exposure time; after 120 min it reached 35–40 T<sup>+</sup>T Mbp<sup>-1</sup> in all three studied cyanobacteria. UV-B had a much more pronounced effect than UV-A on CPD formation in *Nostoc* sp. In this cyanobacterium dimer formation started as early as 30 min of UV-B exposure. UV radiation also induced single- and/or double-strand breaks in various cyanobacterial species.<sup>283</sup> Other effects of UV-B exposure are a rapid inhibition of photosynthesis, as shown in the cyanobacterium *Scytonema javanicum*.<sup>284</sup> The inhibition of photosynthesis in picoplankton (0.2–2  $\mu$ m) and nanoplankton (2–20  $\mu$ m) by solar UV radiation was studied in an oligotrophic high mountain lake in the Swiss Alps using carbon uptake.<sup>285</sup> The study revealed that the assemblages were most affected by UV-A. Picoplankton turned out to be more sensitive than nanoplankton. Also, Li *et al.*<sup>286</sup> showed that UV-B radiation affects the phosphatase activity of the terrestrial cyanobacterium *Nostoc flagelliforme*. Likewise, the uptake of NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, and urea is inhibited by exposure to solar UV-B.<sup>287</sup>

As do marine phytoplankton, freshwater organisms protect themselves against detrimental solar UV radiation and photo-oxidative stress by producing MAAs as well as photoprotective carotenoids.<sup>288–291</sup> Some chlorophytes use sporopollenin or sporopollenin-like substances (algenans), biopolymers of variable composition, for screening solar UV, such as *Scenedesmus communis*<sup>292</sup> and *Chlamydomonas nivalis*.<sup>293</sup> These almost undegradable molecules are linked to the algal cell wall and can be found in zygospores. They absorb in the UV and blue regions of the spectrum and are responsible for the observed UV-resistance of these organisms.<sup>294–296</sup>

## Conclusions

Many studies and predictions have shown that climate change-related variables have an overall common behavior that, for example, includes the increase in temperature and CO<sub>2</sub> in the water column, the increase in solar radiation due to shallower UML, the decrease of nutrients due to isolation of the UML from deep waters with increasing stratification, or the increase of nutrients in coastal areas due to increased continental run off. In this perspective, however, we show that although the general trends are observed, the responses of aquatic primary producers have great variability in the different ecosystems. While an increase in temperature seems to be beneficial in polar waters as it enhances primary production, an indirect negative effect is the decrease of penetration of solar radiation in the water column (and thus limiting photosynthesis) due to melting of glaciers and run off of particles. Nevertheless, this melting of ice and reduction in ice thickness allow extensive blooms of phytoplankton under the ice due to more pene-

tration of solar radiation. In contrast, increased temperature in tropical areas put more stress on cells already growing at the high limit of temperature. It also puts more strength in the pycnocline thus isolating the UML even more and tending to reduce even further the potential input of nutrients from deep waters. Increasing CO<sub>2</sub> concentrations in the water column also have contrasting effects in polar and tropical areas. In general calcified tropical organisms seem to be the most affected. In addition to these few examples, the interaction among factors changes over the aquatic systems; while an increase in temperature seems to counteract (*i.e.*, antagonistic effect) the impact of solar UV radiation in polar and temperate systems, it reinforces it (*i.e.*, synergistic effect) in tropical waters. Moreover, coastal areas and inland freshwater bodies are receiving increasing amounts of particulate and dissolved materials of terrestrial origin, thus changing the underwater light field, and so the exposure of cells in the water column. This latter is also conditioned by wind and depth of the UML. So, overall, we are directing towards a new “disequilibrium” and multiple factors’ interactions should be considered in order to improve our predicted general and regional models of how primary producers would respond to global change and how this would affect the whole aquatic food web.

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