PERSPECTIVE

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The interactive effects of stratospheric ozone depletion, UV radiation, and climate change on aquatic ecosystems

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This assessment summarises the current state of knowledge on the interactive effects of ozone depletion and climate change on aquatic ecosystems, focusing on how these affect exposures to UV radiation in both inland and oceanic waters. The ways in which stratospheric ozone depletion is directly altering climate in the southern hemisphere and the consequent extensive effects on aquatic ecosystems are also addressed. The primary objective is to synthesise novel findings over the past four years in the context of the existing understanding of ecosystem response to UV radiation and the interactive effects of climate change. If it were not for the Montreal Protocol, stratospheric ozone depletion would have led to high levels of exposure to solar UV radiation with much stronger negative effects on all trophic levels in aquatic ecosystems than currently experienced in both inland and oceanic waters. This "world avoided" scenario that has curtailed ozone depletion, means that climate change and other environmental variables will play the primary role in regulating the exposure of aquatic organisms to solar UV radiation. Reductions in the thickness and duration of snow and ice cover are increasing the levels of exposure of aquatic organisms to UV radiation. Climate change was also expected to increase exposure by causing shallow mixed layers, but new data show deepening in some regions and shoaling in others. In contrast, climate-change related increases in heavy precipitation and melting of glaciers and permafrost are increasing the concentration and colour of UV-absorbing dissolved organic matter (DOM) and particulates. This is leading to the "browning" of many inland and coastal waters, with consequent loss of the valuable ecosystem service in which solar UV radiation disinfects surface waters of parasites and pathogens. Many organisms can reduce damage due to exposure to UV radiation through behavioural avoidance, photoprotection, and photoenzymatic repair, but meta-analyses continue to confirm negative effects of UV radiation across all trophic levels. Modeling studies estimating photoinhibition of primary production in parts of the Pacific Ocean have demonstrated that the UV radiation component of sunlight leads to a 20% decrease in estimates of primary productivity. Exposure to UV radiation can also lead to positive effects on some organisms by damaging less UV-tolerant predators, competitors, and pathogens. UV radiation also contributes to the formation of microplastic pollutants and interacts with artificial sunscreens and other pollutants with adverse effects on aquatic ecosystems. Exposure to UV-B radiation can decrease the toxicity of some pollutants such as methyl mercury (due to its role in demethylation) but increase the toxicity of other pollutants such as some pesticides and polycyclic aromatic hydrocarbons. Feeding on microplastics by zooplankton can lead to bioaccumulation in fish. Microplastics are found in up to 20% of fish marketed for human consumption, potentially threatening food security. Depletion of stratospheric ozone has altered climate in the southern hemisphere in ways that have increased oceanic productivity and

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consequently the growth, survival and reproduction of many sea birds and mammals. In contrast, warmer sea surface temperatures related to these climate shifts are also correlated with declines in both kelp beds in Tasmania and corals in Brazil. This assessment demonstrates that knowledge of the interactive effects of ozone depletion, UV radiation, and climate change factors on aquatic ecosystems has advanced considerably over the past four years and confirms the importance of considering synergies between environmental factors.

1   Introduction

The effects of ultraviolet (UV) radiation on aquatic ecosystems and associated security of food and water depend strongly on interactions with climate change including warming, cloudiness, precipitation patterns, ice and snow cover, as well as other environmental factors such as clarity of water, acid-deposition, and acidification of oceans (Fig. 1). These interactive effects control the levels of underwater exposure to UV radiation as well as the ability of organisms to respond to damaging UV through

behavioural avoidance, production of photoprotective compounds, and repair mechanisms. Indirect effects of UV radiation on aquatic organisms are also important through their influence on predators, competitors, parasites, and pathogens, as well as on access to food resources and optimal habitat. For example, one of the most valuable ecosystem services provided by solar UV radiation is that the most damaging, shortest wavelengths also contribute to solar disinfection of waterborne parasites and pathogens that can reduce disease of many organisms. Reductions in the clarity of water associated with natural and
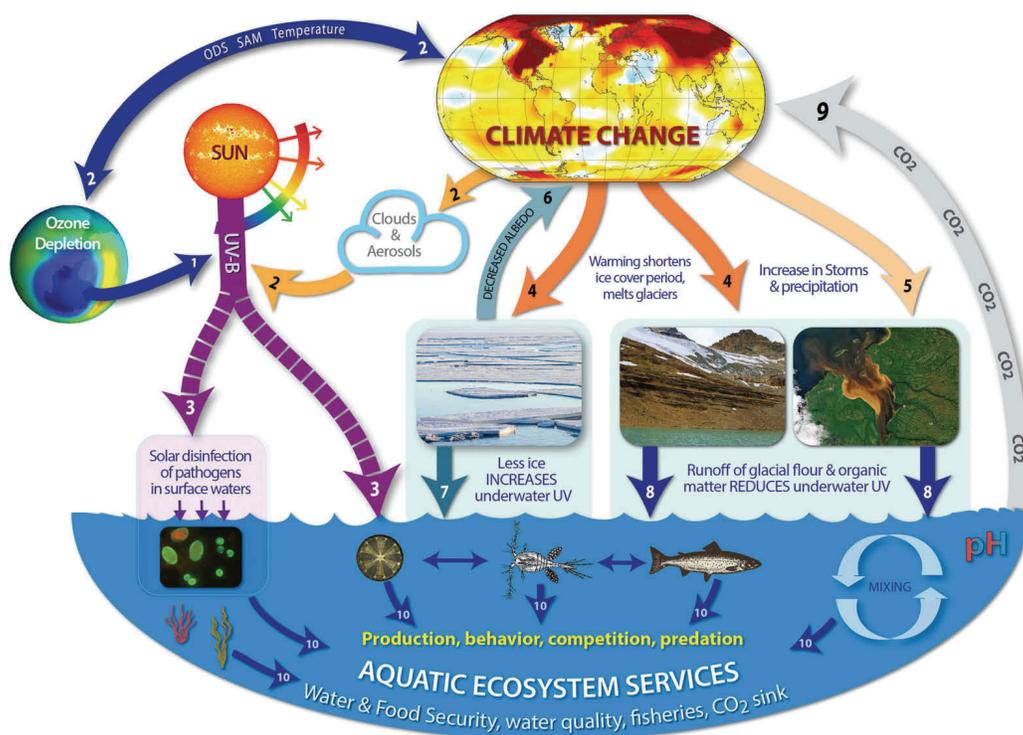

Fig. 1   Conceptual diagram of (1) the direct effects of ozone depletion and (2) interactions with climate change, on (3) the amount of UV radiation that reaches the surface of aquatic ecosystems. Also shown are (4–9) the factors regulating underwater UV exposure and interactions with climate change, and (10) their consequent effects on aquatic ecosystem services. Climate warming is causing (4) shorter duration and thinner ice and snow cover and melting of glaciers, as well as (5) heavier precipitation that increases inputs of terrestrially derived dissolved organic matter (DOM) to aquatic ecosystems in many regions. Droughts reduce runoff and DOM inputs. Reduced snow and ice cover (6) decreases albedo (reflection back into space) and (7) increases underwater UV exposure, while increases in runoff from melting glaciers and increased DOM (8) reduce underwater UV exposure. Increases in atmospheric CO_2 (9) lead to acidification of aquatic ecosystems. Collectively these changes in the transparency of water can alter penetration of visible and infrared light that alter thermal stratification and thus mixing depth and consequent UV exposure of both attached and open-water aquatic organisms (see Fig. 2). Increases in DOM associated with declines in anthropogenic acid deposition and increases in precipitation may (8) increase pH in inland waters, while (9) increases in atmospheric CO_2 can decrease the pH in the oceans and some lakes, altering the role of these ecosystems as sinks or sources of CO_2, and increasing damage by UV radiation of calcifying organisms. These interactions between UV radiation and climate change modify (10, left to right) large algae, pathogens, aquatic food webs, and mixing processes, with important consequences for water and food security. Abbreviations: ODS, ozone depleting substances; SAM, Southern Annular Mode; UV-B, ultraviolet B radiation; CO_2, carbon dioxide (numbers in parentheses refer to the arrows in the diagram).

anthropogenic activities can compromise these critical ecosystem services. Here we provide a current assessment of knowledge about the effects of UV radiation on aquatic ecosystems, emphasising the novel findings since the last United Nations Environment Programme's Environmental Effects Assessment Panel Quadrennial report.[1] We start by assessing recent advances in understanding of the major factors controlling underwater exposure to UV radiation, and then discuss both the beneficial and adverse effects of UV radiation in the context of interactions with climate and other environmental change. We also discuss the unique climatic effects of ozone depletion over Antarctica on aquatic ecosystems in the southern hemisphere and provide an assessment of critical knowledge gaps in our current understanding of the effects of ozone depletion and UV radiation on aquatic ecosystems.

2   Changes in physical ecosystem structure alter exposure to underwater UV radiation

Climate change and stratospheric ozone depletion are changing exposure to UV radiation in marine and inland surface waters through their influence on incident irradiance, ice and snow cover, water transparency, and the depth to which organisms passively circulate. These factors modify habitat structure and the exposure of materials and organisms to solar radiation including UV radiation. The highest exposure levels occur in surface waters. This is especially true for short wavelength UV-B radiation, which is the most damaging per photon, but also the most strongly and selectively absorbed in natural waters. Vertical mixing moves organisms through surface waters of uniform temperature, commonly defined as the mixed layer depth. In inland waters, coastal zones, and open oceans, the mixed layer depths vary seasonally, regionally, and with water body characteristics. In the oceans, mixed layer depths are deeper in winter in polar regions, and shallower in coastal and tropical regions as well as in all waters during the summer.[2] They range from hundreds of meters at the deep, extreme depths, well beyond the penetration of solar radiation, to meters at the shallow extreme, in which exposure to UV radiation can be sufficient to cause significant effects.

The mixed layer depths of inland waters are extremely variable from centimeters to hundreds of meters, and are often deeper in more transparent lakes and reservoirs due to deeper penetration of visible and infrared wavelengths of sunlight.[3–5] Exposure to UV radiation can also be a factor in the vertical distribution of bottom-dwelling organisms. For example, water transparency to UV-B radiation is one component determining the upper depth distribution of marine, especially polar, macroalgae.[6]

2.1   Factors controlling exposure to UV radiation

2.1.1   Incident irradiance. Factors important in controlling incident UV irradiance, including stratospheric ozone, cloudi-

ness, and aerosols, are discussed extensively in ref. 7. Among these, there are some processes that alter incident irradiance that have specific importance to aquatic ecosystems, such as the influence of fires due to intensified droughts. Smoke from fires preferentially filters out UV radiation relative to visible light[8] (see also ref. 7, 9 and 10), affecting many processes. Thus, when winds brought a smoke plume from large California wildfires over Lake Tahoe, zooplankton, which use UV radiation as a depth cue,[11] migrated to shallower depths, potentially affecting their susceptibility to plankton-eating fish predators.[12]

2.1.2   Ice and snow cover. The reduction in extent and duration of ice cover is one of the most widely recognised effects of climate change.[13] Ice cover is thinner and melts earlier than it has in the past in inland and coastal waters,[14–17] and is covering less of the Arctic Ocean.[18] Depending on thickness, snow-cover on ice can prevent most or all UV radiation from entering the water column. Models predict that the decline in ice cover will cause as much as a 10-fold increase in UV-B radiation entering Arctic surface waters.[19] Simultaneously, photosynthetically active radiation (PAR, 400–700 nm) will increase, promoting increased production. Without ice, the water is also affected by wind, which enhances mixing. The increase in exposure to UV radiation can be quite large for higher latitude regions, where the ice-out occurs close to the summer solstice and the annual solar maximum when incident solar radiation is greatest.

Earlier and longer seasonal exposure to UV radiation could adversely affect key marine zooplankton[20] and accelerate the release of CO_2 to the atmosphere by photodecomposition of dissolved organic matter[21] (see ref. 9 for more details on photodecomposition). A related effect of prolonged exposure to sunlight is photobleaching, which decreases the colour of terrestrially derived, dissolved organic matter (DOM), and increases the transparency of water to UV radiation.[22–24]

Around Antarctica, poleward displacement of climate zones is changing the size and distribution of the seasonal ice zones, most notably a loss of sea-ice around the Antarctic Peninsula, along with an increase in sea-ice in the Ross Sea.[25] The direction of this sea-ice change in the future, however, remains uncertain[26] (see ref. 7).

2.1.3   Water transparency. Transparency of surface waters to UV radiation is primarily controlled by the amount of DOM, which, together with other constituents, is also an important regulator of transparency to visible light. DOM is increasing in many temperate waters in the northern hemisphere,[27] leading to decreases in transparency to UV radiation.[28] For example, 68% of 474 lakes sampled in Norway, Sweden and Finland show a median increase of 1.4% per year in total organic carbon (TOC) between 1990–2013.[29] This "browning" is caused by many factors, including increases in precipitation, change in land cover, and the recovery from acid deposition in some regions.[30] Browning is well documented in inland water bodies, such as lakes and reservoirs, with effects at least transiently reaching into nearshore ocean waters.[31–33] The ongoing browning of lakes is projected to continue if precipitation continues to increase,[29] and lakes with a retention time of 1–3

years may be especially affected by climate change-induced browning.[34] Increases in the inputs of terrestrially-derived DOM also increase absorption of longer wavelength visible and infrared sunlight, which warm the surface waters, leading to shallower mixing depths. This is particularly important in small water bodies.[35]

Like DOM, iron-containing compounds selectively absorb UV radiation and have been increasing in many inland water bodies. Increases in concentrations of dissolved iron have been observed in 28% of 340 water bodies examined in 10 different countries across Northern Europe and North America.[36] These increases in dissolved iron are often associated with increases in DOM and similarly contribute to browning of inland waters. Increases in iron likely are contributing to reductions in the UV transparency of inland waters.[37] The role of UV radiation and iron biogeochemistry is addressed in more detail in ref. 9.

Melting glaciers, thawing permafrost, and heavy precipitation events are also major causes of reductions in transparency of water to UV radiation; droughts have the opposite effect on water transparency.[8] Thawing of permafrost is a major source of DOM transported to Arctic lakes and rivers, the latter transporting DOM into the Arctic Ocean.[31,38–41] The transparency of surface waters also decreases due to silty water flowing from melting glaciers.[42–44] Extreme weather, which has increased in frequency with climate change, also affects the transparency of water by increasing runoff and transport of particles to surface waters. Transparency decreases when floods discharge large quantities of DOM and sediment into inland and coastal waters.[29,45–47] On the other hand, drought is associated with increased transparency to solar radiation, including UV radiation, in lakes in both eastern and western United States, including Lake Tahoe.[8]

2.1.4 Mixed layer depth. Many organisms in open-water aquatic systems are planktonic. These are small organisms such as viruses, bacteria, phytoplankton, protozoa and zooplankton, which are passively carried as water circulates both vertically and horizontally in surface waters. Exposure of these organisms to UV radiation depends on their vertical position in the water column, as well as on the transparency of the water. Where it occurs, shallowing of the mixed layer depth can increase exposure of organisms to UV radiation by trapping them near the surface. The mixed layer depth responds to multiple climatic factors undergoing change, most importantly global warming, wind strength and distribution, and inputs from runoff and ice melt.[48] Decreases in the density of surface water due to warming and/or freshwater inputs into oceans encourage formation of shallow mixed layers, while strong winds and/or surface cooling break down density gradients, forming deeper mixed layers.

Early Coupled Ocean-Atmosphere Simulation models of global climate change predicted that global warming would increase stratification and, as a consequence, shallowing of mixed layer depths was expected.[49,50] However, recent examination of long-term trends in observed ocean and mixed layer depths of lakes have not revealed any consistent global long-term trends. Instead, changes are regionally and/or seasonally specific.[48,51] The discrepancy with model predictions is at least partly due to problems in properly incorporating wind-forcing into these models.[52] For coastal or inland waters, the role of weather and land-use changes in altering water clarity and thus the heat budgets can also be important.[5,35] Higher resolution, regional simulations of the Southern Ocean predict latitude-specific changes in marine mixed layer depths, with shallower depths at the northern and southern limits of the Southern Ocean and deeper mixed layer depths in between[53] (Fig. 2). The deeper mixed layer depths are related to the strengthening of zonal winds associated with the dominance of the positive phase of the Southern Annular Mode (SAM), during which the latitudinal gradient in surface air pressure is intensified by stratospheric ozone depletion over Antarctica (Fig. 2 and see section 6, and ref. 7 and 54). Latitudinal shifts in climate zones associated with the positive SAM phase have a number of other consequences for southern hemisphere marine ecosystems, such as affecting nutrient supply to the surface layer and distributions of animals and bottom-dwelling organisms.[53] These effects are discussed in more detail in section 6.

The transparency of water is an important factor controlling mixed layer depth in smaller lakes, particularly those with areas of less than about 5 km^2 (ref. 3–5 and 35) (Fig. 3). As water transparency decreases, visible and infrared light do not penetrate as deeply, confining heating to surface waters, potentially increasing the strength of thermal stratification. Therefore, the phenomenon of browning will likely decrease the mixing depth in many lakes (Fig. 3). However, this does not necessarily translate into increased exposure to UV radiation in the mixed layer because at the same time, UV radiation is strongly absorbed by the DOM. The decrease in the UV radiation from this filtering effect can outweigh the increase in average UV radiation with a shallower mixed layer (Fig. 3). Thus, browning is expected to decrease average exposure to UV radiation in many systems even though the surface layer is shallower.[55]

In summary, the combined effects of global change on exposure to UV radiation vary across different types of aquatic ecosystems. In some cases, exposure to UV radiation is increasing, while in other cases it is decreasing. The implications are multifold. Often, increases in exposure to UV radiation are associated with decreased plankton productivity and survival, while decreases can affect depth distributions (relevant to fisheries), and pathogen and parasite survival (relevant to human health). These responses are discussed in more detail in subsequent sections.

3   UV radiation and interactions with climate change have adverse effects on aquatic organisms and processes but adaptations often reduce damage

UV radiation has been affecting the Earth throughout evolutionary time and organisms have developed adaptations to

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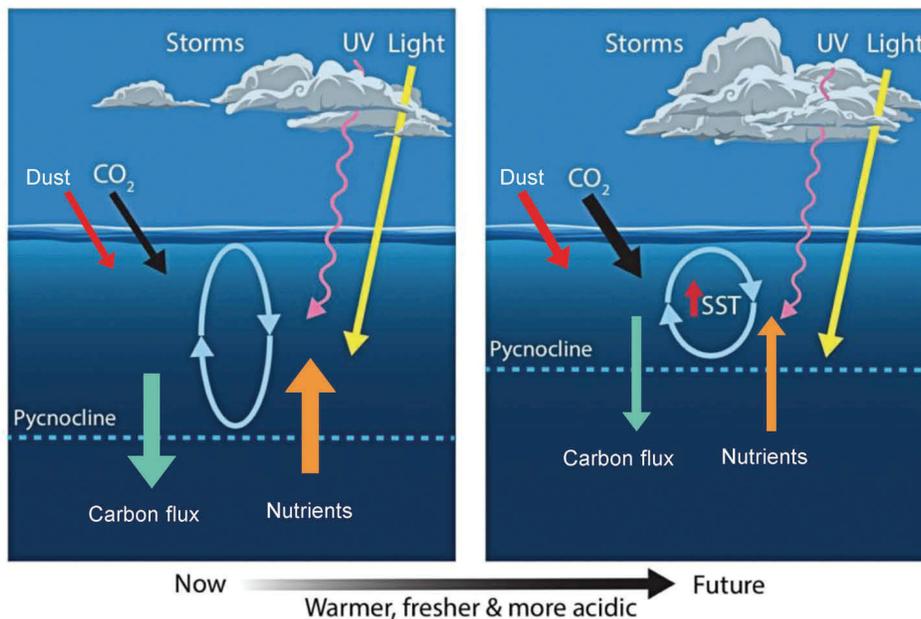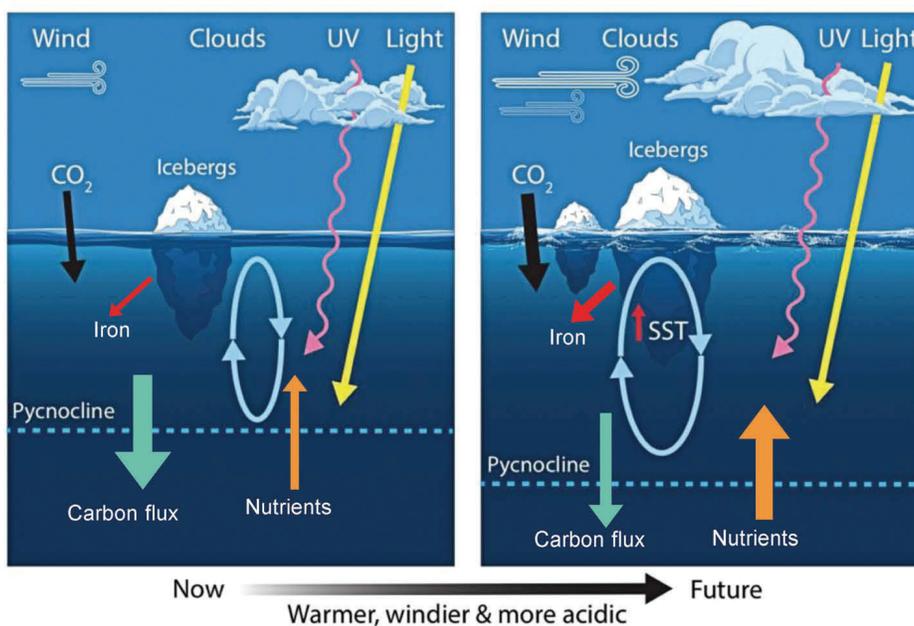

PERMANENTLY OPEN ANTARCTIC ZONE

Fig. 2 Illustration of how the interaction of factors influenced by global change has contrasting effects on sea surface temperature (SST), the density gradient (pycnocline, preventing mixing of surface waters with deeper waters), and exposure to UV radiation in different zones of the Southern Ocean. Climate models predict that the waters in the sub-Antarctic zone will become warmer, fresher, and more acidic, leading to more exposure to UV radiation in the surface layer despite increased cloudiness (top panel). Waters in the permanently open Antarctic zone will experience more acidity but less temperature rise and more wind and cloudiness, leading to deeper mixed layers and on average, less exposure to UV radiation (pink arrow) in the surface layer (bottom panel). After Deppeler and Davidson.[53] CO_2, carbon dioxide.

cope with this threat. The thinning of the stratospheric ozone layer and consequent changes in exposure to UV radiation over recent decades (see ref. 7) has spurred efforts to quantify the adverse effects of UV radiation on aquatic organisms. The variety of behavioural, physiological, and evolutionary responses to UV radiation are also important considerations in quantifying the net effects of exposure to UV radiation at the ecosystem level, including changes in biodiversity.
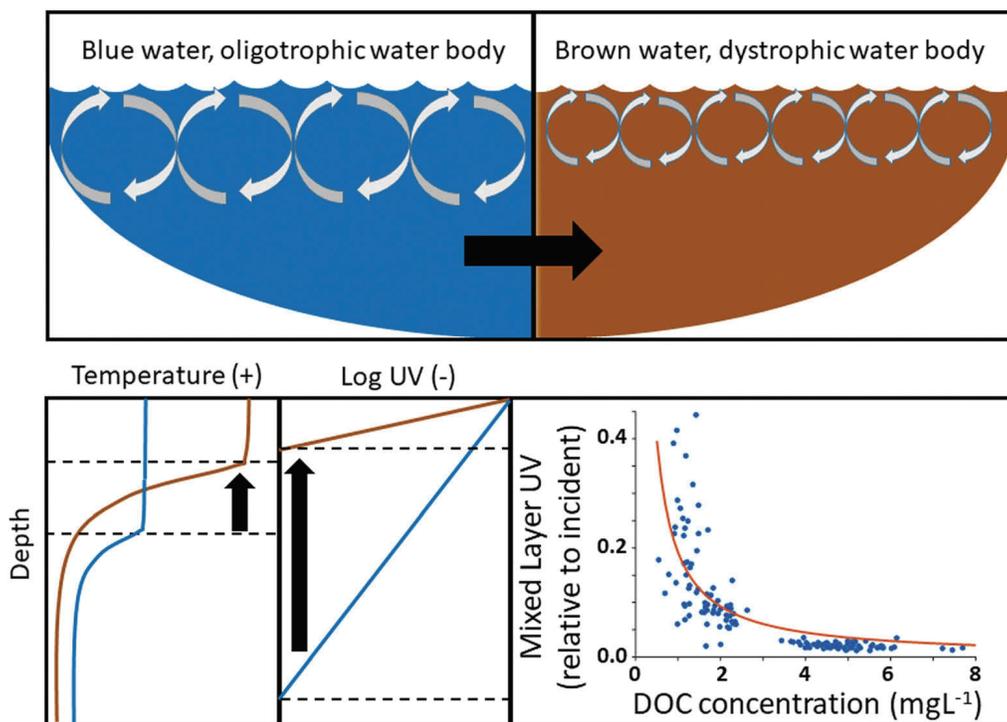
Fig. 3 Browning (increased dissolved organic carbon, DOC) in smaller lakes (<5 km^2) reduces both mixing depth (top and bottom left panels) and UV transparency (bottom middle panels). As the surface layer absorbs more visible and infrared light, heating shifts closer to the surface and the mixed layer depth becomes shallower (short black arrow), affecting temperature profiles. However, UV radiation is more strongly absorbed by the DOC (UV profiles), and the decrease in the depth of penetration of UV radiation from this filtering effect (long black arrow) can outweigh the increase in average UV radiation related to a shallow mixed layer. The plot on the lower right shows average UV irradiance (red line) in the mixed layer (relative to incident UV) *vs.* DOC (blue dots), based on 320 nm-UV profiles, surface layer depth from temperature profiles, and DOC measured in various lakes and times of the year (*n* = 148 samples, mainly from lakes in the northeast region of Pennsylvania, USA, from Williamson *et al.*[28]). Average UV radiation declines steeply over the range of 0−2 mg L^{-1} and much more gradually for concentrations of DOC over 4 mg L^{-1}. The generality of this relationship for other lakes is under investigation.

Several recent meta-analyses confirm and extend our knowledge of the adverse effects of UV-B radiation on all trophic levels in both freshwater and marine ecosystems.[56–58] UV-B-exposure leads to elevated mortality but also sub-lethal adverse effects on reproduction, development, growth, behaviour and metabolism.[56–58]

However, some caution in interpreting these meta-analyses is necessary because many of the studies were conducted in laboratory settings and the spectral composition of the UV treatment was not considered (see also section 3.3.1 of ref. 54 for terrestrial ecosystem examples). Spectral composition is important because shorter wavelengths of UV radiation are many times more biologically damaging per photon than are the longer wavelengths (Fig. 4). The spectral dependence of the impacts of UV radiation differs among biological and chemical processes (Fig. 4). The spectral composition of irradiance in the aquatic environment is also variable, depending on depth and which factors control exposure (Fig. 4). Shorter wavelengths tend to be over-represented in laboratory studies, which generally have shown larger responses (*i.e.*, stronger effects of UV radiation) compared to field studies.[58] Hence, while general adverse effects of UV-B radiation on aquatic organisms have been clearly documented, the strength of

these effects in nature cannot be effectively estimated from experiments with artificial UV radiation unless spectral dependence is also quantified and taken into account. Thus, more attention to the spectral dependence of both exposure and response to solar UV radiation will be required to quantify the long-term effects of elevated UV radiation, especially on trophic interactions such as competition and predation. Shifts in trophic interactions can subsequently result in changes in community structure, ecosystem services, and food and water security.

3.1 Primary producers

Primary producers such as phytoplankton and macroalgae are dependent on sunlight and are therefore also exposed to UV radiation, which can adversely affect their metabolism.[66] These primary producers take up CO_2 and thus act as a potential sink for CO_2 from burning of fossil fuels and other anthropogenic CO_2 emissions. Any significant effects of UV radiation on primary producers, most importantly phytoplankton, will, in turn have direct consequences for the global carbon cycle and climate change. Beyond the targets for damage by UV radiation (DNA, lipids, protein) that are common for all biological systems, a major site of damage
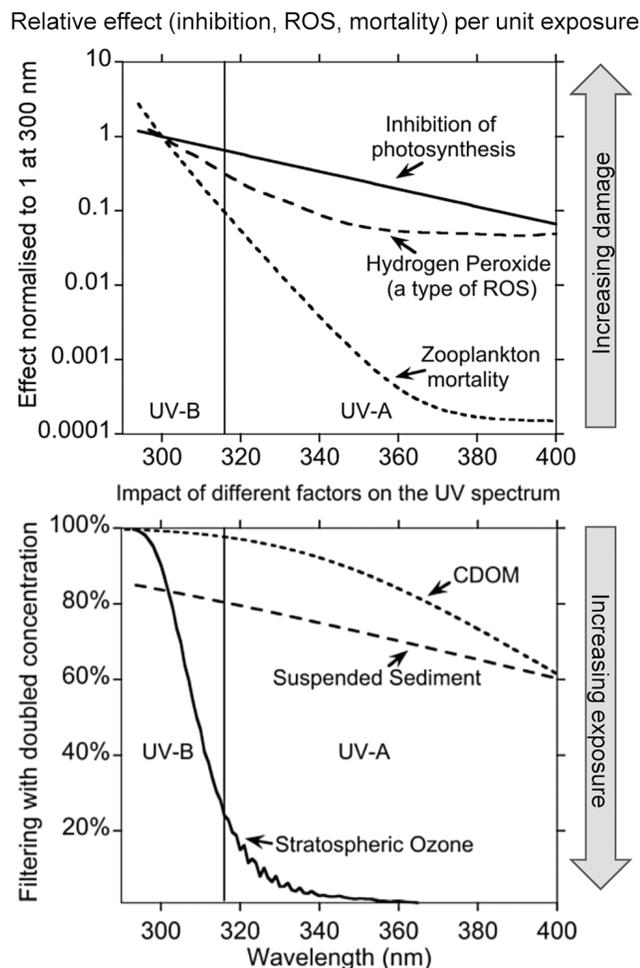
Fig. 4 Spectral variation in some of the effects of UV radiation in aquatic ecosystems (top graph) compared to the spectral change in irradiance caused by different environmental factors (bottom graph). Effects are on a log scale and the wavelength ranges are divided between UV-B and UV-A. The top graph shows examples of the relative effectiveness of UV radiation at a specific wavelength in producing (1) dissolved hydrogen peroxide, a reactive oxygen species[59] (ROS), (2) inhibiting photosynthesis in picocyanobacteria,[60] very small phytoplankton characteristic of the central ocean, and (3) contributing to the mortality of freshwater zooplankton, small invertebrates and larval fish.[61] The bottom graph shows the proportional filtering of UV entering the aquatic environment associated with a doubling of different UV-filtering substances, including stratospheric ozone, which filters incident irradiance,[62] while suspended sediment and coloured dissolved organic matter (CDOM) change water transparency.[63] For example, a filtering effect of 90% means that the doubled concentration has reduced irradiance to 10% compared to the original concentration. Aquatic ecosystems respond to both UV-B and UV-A radiation. Ozone specifically filters out UV-B radiation, while DOM strongly filters out UV-B radiation, but also reduces UV-A radiation and some visible light (wavelengths > 400 nm). Filtering by suspended sediment is not as wavelength-selective and reduces transparency in the UV-A and visible range. The curves are examples drawn from recent research, to illustrate the relative differences in spectral responses within aquatic ecosystems. It should be noted that these responses do differ between organisms and environments (see reviews by Neale and Kieber,[64] Harrison and Smith[65]).

in primary producers is the photosynthetic machinery. This includes photosystem II and the accessory pigments that funnel light energy to the reaction centers.[67] The subsequent damage will directly reduce primary production. Phycobilin pigments, found in cyanobacteria, cryptomonads, and red algae, are especially sensitive. The extent of the effect of UV radiation shows substantial variation among individual organisms.[66,68] In nature, the effects are dependent on the level of exposure to UV radiation, but they are also modulated by temperature[68,69] and nutrients (section 3.3). Since sensitivity to these effects also varies between species and with environment, exposure to UV radiation has the potential to change the composition of communities. For bottom dwelling primary producers (seagrasses, seaweeds, and small algae), the exposure levels to UV radiation will directly follow the ambient exposure levels, which are a function of incident sunlight and water transparency. For plankton, the same factors are important, but in addition, the mixed layer depth determines the mean level of exposure during the vertical circulation. It also determines the duration of high exposure to UV radiation near the surface. Some phytoplankton produce toxic compounds such as microcystins, and blooms of these algae, called harmful algal blooms (HABs), can have adverse effects on other organisms. While the development of HABs is thought to be mostly a function of nutrient supply, HABs may be modified by exposure to UV radiation.[70]

3.1.1 Inhibition of algal photosynthesis and other processes. Many studies have shown that photosynthesis by phytoplankton and macroalgae is inhibited by near-surface solar radiation, with much of the effect caused by UV radiation.[65,71] Earlier work focused mostly on freshwater, coastal, and polar systems. More recently, field experiments have shown that inhibition by UV radiation is also important for algal assemblages at lower latitudes and in the open ocean.[72,73] Exposure to UV radiation also inhibits synthesis of a key organosulfur compound, dimethylsulfoniopropionate, a marine precursor to dimethyl sulfide, a gas that helps ameliorate climate warming through the generation of sulphate aerosols.[73] Laboratory studies continue to investigate how environmental factors affect the response of phytoplankton to UV radiation, and the results of these are discussed in sections 3.2–3.4.

3.2 UV radiation and aquatic primary productivity

A continuing challenge for understanding the importance of the effects of UV radiation on primary productivity of aquatic systems is generalising effects from specific times and locations to the full water column in lakes and over broad oceanic regions. Primary production of the oceans is an important component of the global carbon budget and a critical feedback influencing potential future concentrations of CO_2 in the atmosphere and thus future warming of the climate. This component of the global carbon budget is generally estimated with models, but such models do not currently account for the effects of UV radiation. As a step towards incorporating effects of UV radiation into productivity models, empirical formulas have been developed recently to represent the inhibitory

effects of UV radiation on photosynthesis in key species of phytoplankton in the open ocean.[74,75] Critical to these calculations are biological weighting functions, which provide descriptions of the effectiveness of specific wavelengths of UV radiation for biological processes such as the inhibition of photosynthesis (Fig. 4). Biological weighting functions have been estimated for different growth irradiances and temperatures for each key species, thus enabling the scaling of exposure to UV radiation for inhibition of each species' photosynthetic activity over the global ocean (Fig. 5). Representative areas of the Pacific Ocean were selected to perform full depth-integrated model estimates of primary productivity. Model estimates that included the effects of full-spectrum UV (UV-B and UV-A) radiation were around 20% lower than when UV radiation effects were omitted.[75] Increased UV-B radiation associated with severe stratospheric ozone depletion had little effect on this estimate (<2% additional inhibition).[75] This estimate of the additional inhibition due to the increased UV-B radiation associated with stratospheric ozone depletion is on the low side, but in the same general range (0–6%), as estimates for effects of stratospheric ozone depletion on the productivity of Antarctic and Arctic phytoplankton,[76–78] as well as Antarctic plants.[79]

Further development of these calculations will improve model estimates of open ocean productivity at temperate and tropical latitudes. Global models of primary productivity currently being used have uncertainties that are similar or greater in magnitude than the estimated effect of UV radiation.[80]

In some situations, it is important to consider that exposure of plankton to UV radiation varies greatly on time scales of tens of minutes to hours as water circulates around the surface layer of lakes or oceans (section 2.1). Among the different types of vertical mixing processes, wind-induced Langmuir circulation is particularly important because it is rapid and transports plankton over the full depth of the mixed layer.[2] Thus, phytoplankton can be rapidly (tens of minutes) transported between full exposure at the surface to near darkness at the bottom of the upper mixed layer. In the cold waters of the Antarctic Ocean, UV inhibition and recovery of photosynthesis also occur on scales of tens of minutes to hours.[81] A modeling study compared inhibition of primary productivity in the Ross Sea with and without mixing effects. Inhibition of daily productivity by solar radiation (UV, and PAR, visible light used by plants and algae for photosynthesis), as estimated by the model for conditions during the spring bloom, was about 30% lower with mixing, than without (decreasing from 11% inhibition with no mixing to 7% in its presence).[82] Mixing lessened inhibition because phytoplankton were circulated between the inhibitory near-surface zone and the recovery-promoting irradiance environment of the mid-depth zone. Accurate simulation of Langmuir circulation, however, required a computationally intensive hydrodynamic model, which limits a more general assessment of mixing effects in oceans. Such assessment will be possible if more efficient, yet still realistic methods are developed to simulate vertical transport in the surface layer.

While progress is being made, challenges remain in integrating effects of UV radiation on productivity into modeling frameworks for overall global change. Continuing model development, along with better remote sensing by satellite,[83] will improve the prediction of marine productivity under present and future conditions. This will enhance our understanding of the global consequences of the interaction of UV radiation and other climate change variables including implications for critical marine ecosystem services and food security.
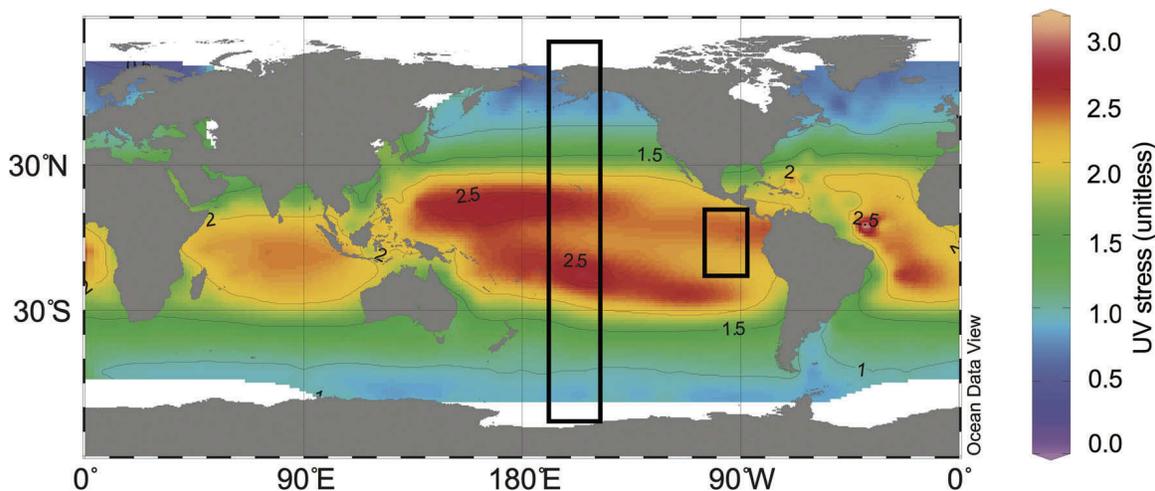

Fig. 5 Distribution of the intensity of UV radiation stress on photosynthesis for the globally important picophytoplankton, *Prochlorococcus*. The metric for UV radiation stress (colour bar) reflects the combined effect of both incident UV radiation and transparency of the ocean on biologically effective irradiance in the water column (1 = moderate stress). The map shows that the combination of these stress factors is greatest in the subtropical Pacific Ocean. The rectangles delimit areas where the impact of this UV radiation on primary productivity was modeled over the full water column, including the effects of inhibition, which lowered the model estimates of average picophytoplankton production in this region by ~20%. After Neale and Thomas.[75]

3.3 Effects of UV radiation are modulated by nutrients

Nutrients modulate the adverse impacts of UV radiation on primary producers because UV-protecting pigments and repair of UV-induced damage require nutrients.[84] Some recent research has assessed how increased inputs of nutrients from aerosols affect sensitivity to UV radiation in phytoplankton communities. Deposition of wind-borne dust from the Sahara is an important source of phosphorus to nutrient-limited phytoplankton in the Mediterranean Sea that, depending on the composition of the community, can either augment or diminish the adverse effects of UV radiation.[85] In offshore waters, the adverse effects of UV radiation were accentuated by deposition of this dust, while in nearshore waters, deposition of dust counteracted the adverse effects of UV radiation. Similarly, the composition of species as well as the occurrence of deposition influences the interaction of dust-borne phosphorus and UV responses in lakes[86] and in oligotrophic coastal waters (see section 6.2.1 for Southern Ocean examples).[87] UV radiation, in combination with additions of phosphorus comparable to those received during a dust event, stimulated the primary producers in a Spanish lake, La Caldera, which receives frequent pulses of dust. This was caused by a trophic shift in mixotrophic plankton (organisms that derive carbon from both photosynthesis and consumption of bacteria) away from grazing (more sensitive to UV radiation) to autotrophy (less sensitive to UV radiation, providing there is enough phosphorus). However; a similar enrichment with phosphorus in another lake, Los Cántaros, in Argentina, produced the opposite result. This community did not have a history of deposition of dust and seemed unable to exploit the increased phosphorus to mitigate effects of UV radiation. However, the trophic shifts of the La Caldera community in response to UV radiation depended on the temporal pattern of dust deposition events. Mixotrophic plankton were less affected by UV radiation in a scenario with a series of smaller dust events *vs.* a single large pulse.[88] Phytoplankton from very low nutrient waters in the coastal Mediterranean Sea were affected synergistically or antagonistically by UV radiation and phosphorus.[87] The interactive effects of UV radiation and phosphorus were positive on photosynthesis, but adverse on overall primary production and phytoplankton biomass because the addition of phosphorus allowed the inhibitory effect of UV radiation to be more fully expressed. These studies underscore that changes in sensitivity to UV radiation are related to availability of nutrients, and this is one of the factors mediating how deposition of dust influences community structure of phytoplankton.

Other interactions between nutrients and effects of UV radiation include the increased sensitivity to UV radiation of cyanobacteria grown with a low supply of iron, a critical micronutrient.[89] Cyanobacteria grown with sufficient iron are less affected by UV radiation presumably because iron is a critical component of cellular mechanisms that control concentrations of intra-cellular reactive oxygen species (ROS), and UV-B-induced ROS are known to induce cellular damage. UV-B radiation is also thought to facilitate the uptake of iron by inducing the reduction of Fe(III) in the water to the more bioavailable Fe(II).[90] In contrast, ocean acidification decreases the bioavailability of iron.[91] Inside the cell, greater concentrations of iron will increase the activity of the antioxidant system needed for scavenging ROS. Estimation of the effects of UV radiation on plankton in areas of high iron concentrations can thus underestimate effects of UV radiation when iron is limited, as in many areas of the Pacific Ocean and Southern Ocean.[89] Nitrogen (N) fixation by cyanobacteria is also important in nitrogen-limited oceans, but it is also inhibited by UV radiation in *Trichodesmium erythraeum*, a cyanobacterium that contributes substantially to nitrogen fixation in marine ecosystems.[92]

3.4 Photosynthetic organisms produce protective pigments that reduce the potential for damage from UV radiation

Aquatic primary producers manufacture pigments that protect against UV radiation and function as antioxidants. In higher plants, including aquatic ones, UV radiation can induce the production of anthocyanins[93] (see also ref. 54). In brown algae, UV radiation induces the production of pigments called phlorotannins, which function as antioxidants[94] and protect against UV radiation.[95] Cyanobacteria, phytoplankton, and macroalgae produce mycosporine-like amino acids (MAAs), chemicals that have a high UV radiation-absorbing capacity and high enough antioxidant capacity that they are used in the cosmetic industry.[96–100] The diversity of MAAs and the cyanobacteria-specific scytonemins and their biosynthesis pathways were recently described.[101,102] MAAs accumulated in red algae under increased exposure to UV-B radiation in Patagonia due to springtime stratospheric ozone depletion[103,104] (Fig. 6).
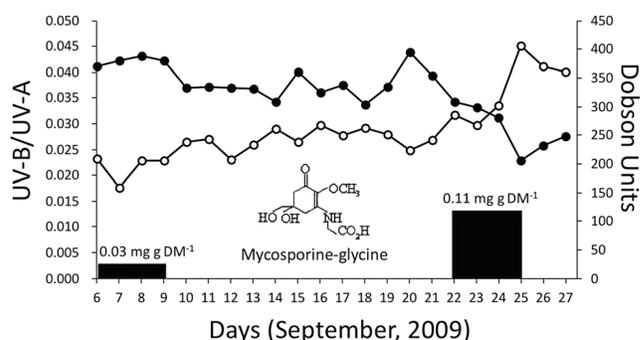

Fig. 6 UV-B/UV-A ratio of incident radiation (open circles) and stratospheric ozone layer (closed circles) expressed as Dobson units, in Punta Arenas (Chile) in September 2009. In the first period (6 to 9 September), the average UV-B/UV-A was 0.021 and the ozone layer 380 Dobson Units, whereas in the second period (22 to 25 September) the average UV-B/UV-A was 0.035 and the ozone layer 273 Dobson Units. This increase in UV-B radiation due to stratospheric ozone depletion was related to an increase in the average content of mycosporine-glycine (a UV-B-photoprotective compound) in the red macroalga, *Mazaella laminariodes*, from 0.03 ± 0.002 to 0.11 ± 0.008 mg g^{-1} dry mass (DM) during these two respective time periods. Modified from Navarro et al.[103]

Enhanced MAA content in macroalgae throughout aquatic environments in Brazil has been shown to be related to a high UV radiation, high pH, and high concentrations of phosphate and nitrate.[105]

The broadest surveys to date of MAAs in marine zooplankton and their food resources were performed in the surface waters of an Atlantic Ocean transect (45°S–50°N).[106] They found MAAs in most surface waters but the concentration was highest from the equator to 30°N where it coincided with the occurrence of the nitrogen-fixing cyanobacterium, *Trichodesmium* (Fig. 7). Analysis of phytoplankton samples taken during the same survey indicated that *Trichodesmium* was the primary source of the MAAs.[106] Generally there was no correlation between MAAs in zooplankton and MAAs in their food resources in the water, rather the highest MAA content was in zooplankton at higher latitudes.

3.5 UV radiation and climate change factors can affect seaweed aquaculture and associated ecosystem services

Coastal environments, including natural seaweed communities, provide a range of important ecosystem services such as sequestration of CO_2, provision of food, and supply of useful chemicals for food, cosmetic, and pharmacological industries[107–110] (see also ref. 54). Global aquaculture of seaweed has increased nearly three-fold between 2000 and 2014 (from 9.3 to nearly 27 million tonnes) and its value has doubled over this period from about USD 3 billion to USD 6 billion.[111] Production of seaweed in natural and aquaculture systems is affected by environmental conditions including light, temperature, and nutrients.[112–114] Studies of the effects of UV-B radiation on seaweeds have focused more on early developmental stages than on mature plants.[84] Interactive effects of nutrient supply and UV radiation show that UV radiation changes macroalgal biomass, community composition, and increases the levels of compounds that protect against UV radiation.[115,116] Thus, UV radiation combined with other environmental variables can affect the quality of food (*i.e.*, commercial seaweeds, or food and shelter for fish).[84,116,117] Corals and calcified algae are potentially more affected by acidification and high solar UV irradiance than non-calcified species; although, in several species, the increase of photosynthetic rate due to increased CO_2 supply can ameliorate the adverse effects of these stressors.[84,95,114] The potential for using seaweed aquaculture as a carbon sink and as a strategy for ameliorating increases in anthropogenic emissions of CO_2 has been proposed.[108,114,118,119]

3.6 Evidence continues to accumulate on the adverse effects of UV radiation on zooplankton, fish, and other aquatic animals

Zooplankton are key components in the aquatic food web, transferring energy from primary producers such as algae to fish populations, and controlling algal abundance and overall water quality. Zooplankton also are essential for sustainable fish stocks, but display reduced reproduction, elevated mortality, behavioural changes, and overall reduced fitness when exposed to UV radiation.[120–126] For example, several species of zooplankton from the Red Sea displayed high sensitivity to solar UV-B radiation,[120] which is striking, since tropical regions are environments with naturally high exposure to UV radiation. Recent laboratory studies also show that UV radiation (340 nm UV-A) can reduce the total number of offspring produced in a common zooplankton species (*Daphnia*) that plays a critical role in freshwater foodwebs.[127] A comparison of lineages from high-UV (high-altitude Bolivia) *vs.* low-UV environments (sea level Swedish lakes) suggests that exposure to UV radiation over an evolutionary time frame has led to *Daphnia* that are adapted to use an early-life, high-fertility reproduction strategy.[127] The mechanistic pathways whereby UV radiation affects physiology were tested in laboratory studies where zooplankton exposed to artificial UV radiation (peak at 306 nm) allocated more resources to repair of DNA in comparison to controls without UV radiation, leading to reduced growth and reproduction in the UV treatments.[128] While these laboratory experiments can be useful in demonstrating mechanisms of damage by UV radiation and response of the organisms, differences in the spectral composition of UV radiation from artificial lamps *vs.* UV radiation in sunlight, preclude extrapolation of these results to nature.

Laboratory experiments with coral reef fish showed that exposure to UV radiation (UV-A, 340 nm) led to elevated respiration and reduced feeding rates.[129] UV radiation (UV-B, 313 nm) also affected swimming performance and metabolic rate adversely in mosquitofish (*Gambusia holbrooki*), especially at suboptimal temperatures.[130] Furthermore, exposure to UV-radiation (at 313 nm) in adult fish increased the susceptibility to disease among the offspring.[130] However, exposure to UV radiation among parental fish also evoked positive effects such as offspring with higher tolerance to UV radiation as a result of reduced damage to cellular components when young were
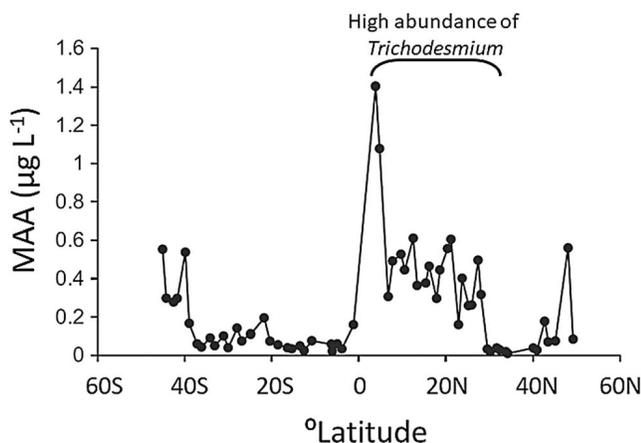

Fig. 7 Latitudinal distribution of photoprotective compounds (total mycosporine-like amino acids, MAAs) in the Atlantic Ocean, showing a region of high abundance of MAAs at low northern latitudes that coincided with high abundance of the nitrogen-fixing cyanobacterium, *Trichodesmium*, between the equator and 30°N latitude. Modified from Fileman *et al.*[106] with permission.

challenged with UV radiation.[130] The rate of growth and calcification in reef-building corals was also shown to be adversely affected by UV radiation in laboratory experiments (340 nm UV-A) and some of the adverse effects were enhanced by simultaneously increased temperatures.[131]

3.7 Some zooplankton species can detect and behaviourally avoid exposure to high levels of UV radiation in surface waters

Some zooplankton species detect and behaviourally respond to UV radiation.[122,125,126,132] Most species tend to avoid UV radiation by downward or horizontal migration but a few also appear attracted to UV radiation; although the behaviours are species- or even population-specific.[125,126,133] The strength of the response is related to size, level of pigmentation, and previous exposure to UV radiation of the organisms.[123,125,126] Behavioural responses to exposure to UV radiation are relatively quick, on the order of seconds and minutes (see also ref. 54, 123, 125 and 134), suggesting that short-term shifts in UV exposure due to changes in cloud cover, sun angle, or other factors, such as UV-absorbing DOM or haze from smoke, can affect the exposure and thus the vertical distribution of zooplankton[12,126,134] and their availability as food for fish (see also ref. 7, 9 and 10 for more on UV radiation and wildfires).

It has been suggested that overall avoidance of surface waters by aquatic organisms is governed by transparency of water, with avoidance of damage by UV radiation dominating in highly transparent waters and avoidance of visual predation in less transparent surface waters.[135] This hypothesis has been evaluated and discussed in several studies.[11,136,137] The intensity of UV radiation explained the amplitude of diel (over a 24 h-period) vertical migration in *Daphnia* during a seasonal cycle.[136] Although this field study cannot differentiate between avoidance caused by UV radiation or by other factors positively correlated with UV radiation (*e.g.*, PAR), experimental manipulation of UV radiation in the field has demonstrated the importance of this radiation.[11,138] Zooplankton tended to avoid surface waters more in lakes with greater exposure to UV radiation than in those with less exposure.[11,137] Vertical distribution of zooplankton also shifted in a lake where transparency varied over time.[11]

3.8 Zooplankton, fish, and other animals have physiological adaptations to reduce potential damage from UV radiation

Evidence continues to accumulate that, apart from avoidance behaviour, zooplankton have several other defense mechanisms to prevent excessive damage by UV radiation. The UV-exposure in Arctic waters is rapidly increasing due to reduced sea-ice (see section 2.1), with consequences for zooplankton and their ecosystem services. For example, the copepod zooplankton genus, *Calanus*, is essential in supporting the North Atlantic Ocean and Arctic Ocean fisheries.[139,140] *Calanus* species in the Arctic generally over-winter in deep water and ascend to shallow waters during spring to feed on algae that grow in the spring-early summer. It was shown that *Calanus* accumulate UV-protective compounds such as MAAs from their algal diet in synchrony with ice-out.[20] This suggests an

efficient UV-protection among *Calanus*, but it is not known if this adaptation will remain effective if ice-out, and hence exposure to elevated UV radiation, come earlier in the season.

Accumulation of carotenoids, such as astaxanthin, is another adaptation among zooplankton to avoid damage from UV radiation. These substances are accumulated by copepod zooplankton when exposed to UV radiation (artificial 340 nm UV-A).[141] However, these substances may also accumulate for other purposes and do not necessarily indicate a response to UV radiation. For example, carotenoids can be coupled to fatty acid metabolism during winter when UV radiation is absent or very low.[142] Furthermore, concentrations of carotenoids in Arctic *Calanus* were not correlated with levels of UV exposure.[20] On the other hand, the highest carotenoid levels may occur concurrently with abundant UV-protective MAAs.[143] Hence, the role of carotenoids as UV-protective compounds is uncertain. Either way, carotenoids are strong antioxidants and are believed to have several beneficial functions in organisms exposed to UV radiation.

Other important zooplankton, such as the cladoceran *Daphnia* spp., have elevated melanin concentrations in their outer shell to avoid damage by UV radiation.[144,145] Melanin found in lake sediments has been measured to estimate historic UV radiation exposure coupled to environmental change (see ref. 54 for details on other paleoproxies).[146,147] Aquatic insects such as damselflies also accumulate melanin upon exposure to UV radiation (UV-A, 340 nm), but at a cost of delayed metamorphosis to the adult stage and a smaller body size[148] suggesting fitness costs associated with exposure to UV radiation. When exposed to solar UV radiation, amphipods (crustaceans) accumulated photoprotective compounds (determined by absorbance peaks of extracts between 310–360 nm) from their diet of seaweed.[149]

Further adaptations to avoid UV-induced damage were studied by Connelly *et al.*[124] demonstrating that *Daphnia* supplied with vitamin D3 survived better under laboratory exposure to UV-A radiation (340 nm) than controls without UV-A, but the mechanism for this positive effect is not known. Some zooplankton, such as copepods, can also defend themselves against UV radiation by inducing heat shock proteins. These proteins reduce cellular damage by stabilising proteins during seasons of high exposure to UV radiation.[143]

3.9 Reactive oxygen species produced by UV-DOM interactions have localised impacts

UV radiation damages DNA and other cellular structures directly, but it can also indirectly cause damage *via* the production of ROS, which in turn damage the same cellular constituents. The production of ROS is increased when DOM is exposed to UV radiation.[150] The concentrations of DOM have been increasing in recent years in many lakes and coastal zones (section 2.1), which is likely altering the depth distribution of ROS production. It has been demonstrated that ROS can damage DNA in *Daphnia*, and reduce bacterial and some phytoplankton production.[150–152] Laboratory studies with 340 nm UV-A lamps have implicated ROS in the possible inhi-

bition of uptake of dietary nutrients in *Daphnia*.[153] However, recent models suggest that damaging concentrations of photo-produced ROS, in the form of hydrogen peroxide, likely occur only in the top few centimeters of most lakes.[154] Additionally, ROS break down very rapidly. Thus, long-term damaging ROS exposure is unlikely in nature due to wind-driven mixing of the water column and the high attenuation of UV radiation in systems with elevated DOM concentrations (Fig. 3). For example, field measurements of aquatic insect larvae (*Chaoborus*) showed 50 times lower damage of DNA in insects from a high DOM pond compared to those in a low DOM pond.[155] Overall, these data suggest that UV-shading by DOM outweighs the elevated ROS production due to increased DOM concentrations, reducing net damage to aquatic organisms (see also section 2.1). Some potential exceptions where ROS may be more important are in very shallow systems, in surface waters during periods of no wind, or *via* biological production during intense phytoplankton blooms.[156–158]

3.10 UV radiation can affect interactions among species and composition of communities

Few studies examine the effects of UV radiation on multiple trophic levels at the same time, taking into account trophic interactions and differential tolerance to UV radiation among species. The susceptibility to UV radiation is species-specific and may be important in structuring the composition of zoo-plankton communities.[159,160] Field surveys of zooplankton communities suggest shifts in species composition with changing exposure to UV radiation.[160] However, incubation of zoo-plankton communities in different UV radiation environments for several months suggests that UV radiation has only minor effects on overall community composition, and field patterns could also be explained by coincidental changes in other factors such as temperature.[160,161]

Although a recent meta-analysis suggests that the adverse effects of UV radiation are, on average, equally damaging to all trophic levels,[58] this is not always the case. Evidence shows that changes in UV radiation can alter species interactions and community composition in aquatic ecosystems, and that climate change may be indirectly causing these changes in exposure to UV radiation. For example, a common predatory insect larva, the phantom midge (*Chaoborus nyblaei*), is relatively sensitive to UV radiation, in part because it has a transparent body. Recent research shows that this predator appears to be increasing its range among shallow alpine ponds where UV-absorbing concentrations of DOM are high.[155] Concurrent with the spread of this midge, their prey, the relatively more UV-tolerant fairy shrimp (*Branchinecta paludosa*), is being reduced.

Changes in the UV radiation environment will occur in response to changes in absolute radiation but are even more likely *via* climate-induced changes in the amount of UV-absorbing substances (*e.g.*, DOM) in the water column (section 2.1). For example, *in situ* experiments in mesocosms (large enclosures placed in a lake) that simulated the inflow of DOM revealed that DOM stimulates the microbial food web by pro-

viding nutrients, while reducing the damaging exposure to UV radiation,[61] as well as leading to shifts in the structure of the zooplankton community through both direct and indirect effects on UV radiation.[162] Shifts in the overall species composition in response to UV radiation are most likely limited to highly transparent and/or very shallow aquatic ecosystems due to the high UV-absorbing capacity of DOM.

4 UV radiation provides valuable aquatic ecosystem services that are being compromised by reductions in water clarity

In recent decades, stratospheric ozone depletion has led to widespread concerns regarding the adverse effects of elevated exposure to short wavelength UV-B radiation. There are, however, some beneficial effects of UV radiation that will be compromised due to both the recovery from stratospheric ozone depletion and the acceleration of climate change. For example, just as solar disinfection (SODIS) is used to purify drinking water in plastic bottles, and artificial UV radiation is used to disinfect drinking water in municipal supplies such as New York City, NY, and Cincinnati, OH, USA, the UV radiation in sunlight can disinfect surface waters of parasites and pathogens, thus reducing the transmission of waterborne diseases (see also ref. 9). Many human pathogens as well as pathogens of aquatic organisms are inactivated by exposure to UV radiation, and even by short wavelength PAR in solar radiation.[163,164] This valuable ecosystem service is threatened by increasing concentrations of DOM, because DOM selectively absorbs the most powerfully disinfecting short wavelength UV-B (Fig. 4). Modeling the potential for UV inactivation has shown that surface waters with higher concentrations of DOM can reduce the solar disinfection potential of the solar UV-B radiation by tenfold or more.[164] In regions where water transparency has declined, reductions in underwater exposure to UV radiation may thus threaten global health and contribute to the spread of infectious diseases. One important caveat here is that some pathogens may be inactivated by ROS produced by the indirect effects of UV radiation on DOM (section 3.9 and Fig. 10 in ref. 9 and related discussion). In some cases, increases in DOM may not reduce solar disinfection and may even increase it for pathogens that are more sensitive to inactivation by ROS than to direct DNA damage (see ref. 9).

Climate change is altering exposure to UV-A as well as UV-B radiation in aquatic ecosystems through changes in ice cover, increases in DOM, and reductions in the depth of mixing of the surface waters (section 2.1). UV-A radiation has beneficial effects that include contributing to photoenzymatic repair of UV-B-damaged DNA.[165] UV-A radiation is also important in orientation and foraging in many aquatic organisms such as fish and zooplankton that have UV-A photoreceptors. Foraging rates were higher for freshwater largemouth bass in the pres-

ence of UV radiation (<400 nm) than when it was absent under natural field conditions.[166] Similarly the importance of UV radiation for foraging success has been demonstrated in zebrafish in the laboratory, by comparing mutants with few UV receptors (cone cells) to normal zebrafish with abundant UV cone cells.[167] In contrast, laboratory experiments with bluegill sunfish[168] show no evidence of UV-enhanced foraging, and laboratory experiments with a reef fish show that UV radiation from artificial lamps (<400 nm) can actually reduce foraging success.[129] A potentially important interaction is that, at higher concentrations, DOM may reduce the visual field (reactive distance) of fish in addition to reducing the penetration of UV radiation. Thus, depending on the fish species and optical conditions, UV radiation may either enhance or inhibit foraging. These differences may be species-specific or vary due to differences in either the intensity or the spectral composition (wavelengths) in natural vs. artificial sources of UV radiation. Regardless of the effects of UV-A radiation on foraging, the ability to detect and avoid UV-A radiation has the potential to allow aquatic animals, including small, transparent, young fish in their first year of development, to avoid more damaging UV-B that does not penetrate as deeply in the water column as UV-A radiation. This ability of aquatic organisms to avoid damage by UV radiation has the potential to increase survival rates and year class strength of both recreationally and commercially valuable fish species.

Another beneficial effect of solar UV radiation lies in the photo-degradation of DOM, which provides a source of more bioavailable fixed carbon and nutrients that can stimulate aquatic food webs. Photo-degradation has been demonstrated to be particularly important in Arctic surface waters, which are receiving DOM released into runoff water from thawing permafrost.[169] This is, however, a double-edged sword. While photo-degradation has the potential to stimulate ecosystem productivity, it also releases greenhouse gases through the conversion to a bioavailable form of terrestrially-derived fixed carbon that has been locked up in permafrost for millennia or longer, thus aggravating climate warming (see ref. 9).

5 Effects of UV radiation are highly dependent upon interactions with other aspects of environmental change

5.1 Acidification of oceans changes responses of aquatic organisms to UV radiation

Increasing amounts of CO_2 in the atmosphere due to human activities result in higher concentrations of CO_2 in open oceans, but the net changes in the water depend on the mixing dynamics. The oceans are a major sink for anthropogenic emissions of CO_2.[170] CO_2 reacts with water to produce carbonic acid, which dissociates into a carbonate ion and two protons, thereby decreasing the pH. This acidification has adverse effects on some aquatic organisms and their protec-

tion from damage by UV radiation, as described in more detail below.

A 30% increase in protons results in a reduction of pH by 0.1 units, and acidification of oceans is predicted to reduce the pH by 0.3–0.4 units by year 2100 under a business-as-usual scenario (RCP8.5).[171] Some inland reservoirs and larger lakes are either already showing, or expected to show decreases in pH similar to those observed in the oceans.[172,173] In contrast, however, the recovery of many inland waters from acid deposition (e.g., acid rain), has increased the pH of some inland waters by up to a full pH unit in regions of Europe and North America.[27,28] The close proximity of human activity to lakes, and the larger ratio of catchment area : water surface area of most lakes vs. oceans, suggest that future changes in the pH of oceans will be affected by atmospheric CO_2, while the pH of inland waters such as lakes and reservoirs will be more sensitive to other factors related to climate change and land use.

Acidification of oceans alters water chemistry, affecting primary producers differently depending on latitude and other environmental drivers such as solar UV radiation, temperature, nutrients, and concentrations of CO_2.[71,174–176] Some harmful algal species have a low sensitivity to solar UV radiation and, consequently, increasing exposure to UV radiation favours them, resulting in more harmful algae. These shifts may be increased by higher temperatures and nutrients.[177] The interacting effects of ocean acidification and higher temperatures can also stimulate the synthesis of toxic substances, as found for one harmful algal species.[178]

Many phytoplankton, macroalgae, and animals produce calcified exo- or endoskeletons that are thought to have several functions, including protection against predators and solar UV radiation.[179] For photosynthesising organisms this requires about a third of the cell's photosynthetic energy. However, this strategy has been successful as indicated by the wide distribution and biomass production of ecologically important organisms such as calcifying algae (e.g., coccolithophorids). Ocean acidification reduces calcification in aquatic organisms, potentially exposing them to increased solar UV radiation.[174,180,181] Because of the different reactions of particular species or populations to decreasing pH, interactions between UV radiation and ocean acidification may produce shifts in biodiversity and community structure, affecting grazers and fisheries.[182]

5.2 UV radiation interacts with artificial sunscreens, plastics, and other pollutants with adverse effects on aquatic ecosystems

UV radiation interacts with a wide range of pollutants in aquatic ecosystems (see also ref. 9). In some cases, UV radiation enhances the potential toxicity of pollutants via photochemical reactions. In most cases, UV radiation degrades and removes pollutants, changing their chemical composition and sometimes making them less harmful. For example, mercury is a key contaminant in many freshwaters. The toxicity and transport of mercury up the food web to fish occurs through uptake of methylmercury. UV-B radiation dominates the

photo-demethylation process,[183] and the fraction that is photo-demethylated varies between 25% to 80% depending on water transparency.[184] Exposure to UV-B radiation thus reduces the uptake of mercury to fish. Exposure to UV radiation can also increase the toxicity of contaminants such as some pesticides and polycyclic aromatic hydrocarbons (PAHs) to aquatic organisms such as fish and amphibians.[185–187] Some pollutants can negatively affect the ability of aquatic organisms to detect and respond to damaging solar UV radiation. For example, amphibian tadpoles that normally behaviourally avoid damaging solar UV radiation do not avoid it when exposed to the pesticide endosulfan which was widely used in the past.[188]

Two emerging pollutants of concern that interact with solar UV radiation include sunscreen compounds and microplastics (plastic particles < 5 mm diameter). Sunscreen compounds are chemicals that absorb or reflect solar UV radiation and are commonly classified as either organic (e.g., oxybenzone) or inorganic (TiO_2 or ZnO). Carbon-based and inorganic sunscreens can be toxic to aquatic organisms, and can impair the development of corals,[189,190] sea urchins,[191] and fish,[192] as well as affect gene expression[193] and development in bottom-dwelling freshwater insect embryos and larvae.[194] These compounds are widely used in a variety of personal care products and have demonstrated benefits for human health and protection against the damaging effects of UV radiation (see ref. 195). However, these compounds and their metabolites are found in many aquatic ecosystems and researchers are just beginning to identify and understand their environmental effects. Highlighting the growing public awareness of potential adverse ecological effects, the US State of Hawaii recently passed a bill, which will go into effect in 2021. The bill bans the sale and distribution of sunscreens containing oxybenzone and octinoxate due to their negative environmental impacts, especially on corals.[196] Other legislation has been submitted to the European Union that calls for a ban on oxybenzone-containing sunscreens.[197] MAAs found in phytoplankton and macroalgae (section 4.3.6) serve as natural UV sunscreens, and may have potential as alternative sunscreens for humans[98,198] (see also ref. 195).

UV sunscreen compounds have been found in freshwater, coastal, and marine ecosystems in many different regions and countries.[199–201] Environmental concentrations of UV sunscreen compounds can vary widely,[200,202,203] with nearby population density being an important predictor of environmental concentration.[204] Concentrations can be especially high near swimming beaches and waste-water discharge sites,[200,201] but detectable concentrations are also found in remote areas such as the Arctic.[200]

One challenge is that not all studies of potential impacts are conducted at ecologically realistic concentrations.[205] Despite these limitations, recent studies highlight the ways in which sunscreen compounds might impact aquatic food webs and exacerbate other regional or global environmental problems. For example, sunscreens can cause bleaching of coral and death, even at concentrations found in nature, and

at least 10% of reefs might be sensitive to such impacts.[190,206]

The main mode of action of sunscreens on corals appears to be induced oxidative damage, which is enhanced when the compounds are exposed to solar radiation.[189,207] A few studies indicate that certain organic sunscreens may also be endocrine disrupters.[208,209] Some organic sunscreens are known to bioaccumulate in the muscle and lipids of organisms.[210] Adverse effects of organic sunscreens have been identified across a wide range of aquatic taxa such as phytoplankton, protozoa, crustaceans, and fish.[189,202,203] Common inorganic sunscreens such as TiO_2 and ZnO nanoparticles have been found to inhibit the growth and photosynthesis of marine phytoplankton,[211,212] as well as decreasing the survival and reproduction of grazing zooplankton,[213] and, therefore, may adversely impact fisheries. Because species have differential sensitivities to these commercial UV-absorbing compounds, sunscreens may shift the relative species composition in affected aquatic ecosystems.[202,207] However, because adverse impacts vary across taxa, predicting the net effects on ecosystems is difficult.

In addition to some sunscreens, UV radiation may exacerbate the environmental impact of other pollutants such as plastics. On the order of 5 to 10 megatons of plastics are dumped or washed into the oceans each year. Exposure of larger plastic pieces to UV radiation and consequent photo-oxidation is the most important process initiating the formation of microplastics in the marine environment[214,215] (see also ref. 216). The relative costs and benefits of degradation of plastics by UV radiation are still unknown in terms of food security and ecotoxicological consequences. Surveys have revealed that about 20% of marine fish in seafood markets contain microplastics, creating a potentially emerging threat to food security.[217] The impact of potential exposure to UV radiation on the degradation and fate of plastics in aquatic ecosystems depends on whether they float or sink, because this will determine the levels of UV radiation to which they are exposed, and thus the rate of photo-degradation. Higher density plastics such as polyvinyl chloride (PVC) and polyethylene terephthalate (PET) sink to the bottom where low exposure to solar UV radiation reduces photo-degradation.[215] Substantial amounts of buoyant plastics float in surface waters where they are transported worldwide, with extensive pollution even in remote oceans and beaches. Plastics degrade very slowly and can persist in natural environments for decades.[215] However, only about 1–10% of the plastics dumped into oceans annually remain in the surface waters.[218] Thus there is an open question about the overall importance of solar UV radiation in contributing to the breakup and decay of plastics, or how much changing levels of UV radiation alter the cycling of plastics in the global oceans.

Exposure to high levels of solar UV radiation can degrade plastics into smaller microplastic particles (<5 mm, Fig. 8) or even smaller nanoplastics (20–1000 nm; see also ref. 216). The primary concerns about microplastics are (1) that they are contaminants that may be toxic to plankton, the fish that ingest them,[219] and potentially humans, and (2) the presence of posi-

Fig. 8 Plastics are a pervasive pollutant in marine ecosystems, as seen here on Whitsand Beach, Cornwall, UK (left). Both UV radiation and aquatic biota play a critical role in the creation, fate, and toxicity of plastics. UV radiation is the primary environmental factor creating smaller microplastics that are ingested by copepods, the most abundant grazers in the world's oceans. Copepods can in turn serve as a conduit to fish and other seafood consumed by humans; or their fecal pellets, which may contain microplastics (right, with fluorescent microplastics shown for visibility), can contribute to the sedimentation of these plastics to deeper oceanic environments. Photographs by Dr Matthew Cole. Right photo from Clark et al.[218] with permission.

tively buoyant microplastics may slow the sinking of organic carbon to oceanic depths, thus decreasing carbon sequestration in the deeper ocean layers.[220] Microplastics are ingested by zooplankton and may settle out to the bottom of lakes and oceans in their fecal pellets, or be transferred to higher trophic levels including fish.[215,218] Copepods (small crustaceans) are the most abundant zooplankton grazers in the world's oceans and a key link in oceanic food webs. Both copepods and some fish that feed on copepods are important in the biological pump that transfers organic carbon to the deep ocean by vertical migration or settling of fecal pellets. On the order of 73% of mesopelagic fish examined from a warm-core eddy in the Northwest Atlantic contained microplastics.[221] Although not as well-studied as microplastics in the oceans, initial studies indicate that microplastics are as prevalent in many freshwater ecosystems on several continents as they are in the oceans.[222] Nanoplastics in the 50 nm size range have been shown to be ingested by the common freshwater zooplankton *Daphnia*, and transferred to fish through the food web where they in turn accumulate in the brains of fish and can alter their feeding behaviour.[223] This study used manufactured polystyrene particles, and it is unknown whether these particles respond similarly to nanoplastics found in the environment. *In vitro* studies with human cells have shown cytotoxic effects of micro- and nanoplastics, as well as the ability of particles less than 10 μm to carry toxic metals such as mercury and also cross the blood–brain and placental barriers.[224] However, our knowledge of the role of microplastics and nanoplastics is in its infancy, and more information is needed on the extent to which they may serve as a conduit of plastics and other toxins to the seafood supply of the world's markets, potentially threatening human health and food security.[224,225]

6 Effects of stratospheric ozone depletion on climate and aquatic ecosystems in the southern hemisphere

In addition to its direct effects on incident UV-B radiation, stratospheric ozone depletion has resulted in major changes in southern hemisphere climate, affecting atmospheric and oceanic circulation (see also ref. 54), with consequent effects on aquatic ecosystems. The changes in climate are captured by the Southern Annular Mode (SAM, an index of atmospheric variability, which equates to the difference in mean sea level pressure between 60°S and 45°S). Increasing greenhouse gases and ozone depletion over Antarctica have both pushed the SAM towards a more positive phase (greater latitudinal difference in pressure), and the SAM index is now at its highest level in at least 1000 years.[226] Section 2.1.4 discussed how the trend towards a more positive phase of the shifts in SAM have latitude-specific effects on exposure to UV radiation. The following section considers additional climatic effects other than exposure to UV radiation.

6.1 Changes to oceanic circulation

The increasingly positive SAM is manifest in a poleward shift and/or strengthening of the mid-latitude surface wind, which, in turn, plays a fundamental role in ocean circulation. In general, the prevailing westerly wind in the middle latitudes acts to drive northward transport in the underlying ocean (Fig. 9). This creates a region of upwelling on the poleward side (around 60°S), and surface transport towards the equator into the sub-Antarctic zone (between middle latitudes and subtropical zones)[227] (Fig. 9, see also ref. 54). This circulation is
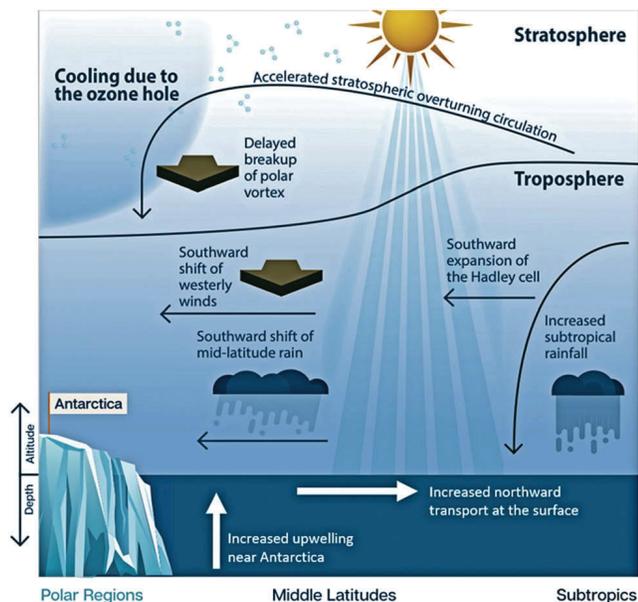
Fig. 9 Cross-section showing the effects of depletion of ozone on circulation in the Southern Ocean. See text for details. Modified from ref. 229.

intensified and shifted south during the positive phase of the SAM, which models suggest is due to the combined effects of stratospheric ozone depletion over Antarctica and climate change. For the austral summer, modelled trends in the vertical ocean circulation are mainly attributable to stratospheric ozone depletion.[228] Depletion of ozone was found to be responsible for the subsurface cooling north of 35°S (*i.e.*, transition between the sub-Antarctic and subtropical zones), with increasing greenhouse gases as the main driver of warming at higher latitudes.[228] In conjunction with warming, the Southern Ocean has largely become fresher (less salty) which is attributed to increased precipitation and runoff.[228]

The most recent scientific assessment of stratospheric ozone depletion[229] concludes that there is evidence for large effects of stratospheric ozone depletion on Southern Ocean atmospheric and oceanic circulation, temperature, and salinity. However, some modelling studies suggest that the contribution of the ozone 'hole' to warming and freshening of the Southern Ocean water is smaller than that of greenhouse gases (likely on the order of 30% or less). Changes in circulation also affect sea-ice extent and duration (for details see ref. 7); however, the role of stratospheric ozone depletion in recent trends of Antarctic sea-ice remains a highly debated topic[229] (see ref. 7).

6.2 Ecosystem and population impacts from changes in atmospheric and oceanic circulation associated with stratospheric ozone depletion and the positive Southern Annular Mode

6.2.1 Changes to ocean carbon uptake. The Southern Ocean plays a very important role in the global carbon budget by absorbing CO_2 from the atmosphere and sequestering it in

the deep ocean, thus reducing the rate at which CO_2 is increasing in the atmosphere.[230] The positive SAM phase reduces net oceanic uptake of CO_2 from the atmosphere and the ocean's ability to sequester it in the deep ocean by altering large-scale ocean circulation.[227,230,231] Partly, this is due to the upwelling of deep water that already has high amounts of CO_2 and cannot absorb more. Additionally, the positive SAM phase affects primary productivity through changes in light and nutrients, some the consequences of which are illustrated in Fig. 2 (see also Deppeler and Davidson[53]). These, in turn, alter how much CO_2 phytoplankton can absorb from surface waters and sequester as organic carbon. The direction of these changes differs by latitude as does the overall effect on productivity, so the net outcome of the positive SAM phase on the ocean biological uptake of CO_2 is variable. In the sub-Antarctic zone, long-term warming and a shallower mixed layer depth are believed to reduce primary productivity by reducing transport of nutrients from deep waters into the surface layer, despite higher availability of PAR (Fig. 2, top panel). However, where the main limiting nutrient, iron, is available, (*e.g.*, in the South Atlantic), increased exposure to PAR can increase primary productivity. Stronger winds and drier conditions associated with positive SAM can also enhance iron concentrations in the ocean by transporting more dust to the ocean from terrestrial sources, such as South America (Fig. 10 and Table 1).[227,231,232] Consistent with this, there has been a long-term trend of increasing phytoplankton biomass in the South Atlantic sector of the sub-Antarctic zone, but decreasing biomass in other areas lacking iron inputs.[233] At about 60°S latitude, increased wind speeds are deepening the mixed layer depth, reducing light, and increasing upwelling and iron availability (Fig. 2, bottom panel). Models differ as to whether the long-term outcome of these increased wind speeds will be an increase or a decrease in productivity[53] and the empirical data are limited. A comparison of observed trends with predictions using a model (CMIP5, Coupled Model Intercomparison Project 5), based on the IPCC scenario RCP8.5, suggested that phytoplankton biomass has been decreasing in the latitudinal band between 50° and 60°S.[233]

Long-term decreases in duration and extent of sea-ice are expected due to the combined effects of global warming and the positive SAM phase. In addition to the effects of warming temperatures, increased ocean upwelling erodes the bottom of sea-ice, which results in substantial declines in sea-ice around the Antarctic Peninsula. However, in the short-term, northward transport is extending the sea-ice zone where upwelling is weaker, for example, in the Ross Sea.[53] Where sea-ice has been decreasing, phytoplankton biomass has increased at the expense of sea-ice algae.[53,233] The main ecosystem impact of changes in sea-ice may be through changes in the timing and composition of primary production, which controls other ecosystem aspects such as fisheries, birds, and mammal populations in both marine and freshwater ecosystems (see Table 1).

6.2.2 Seabirds, marine mammals, and marine ecosystems. Together with climate change, the effects of stratospheric ozone depletion on Southern Ocean climate can have diverse
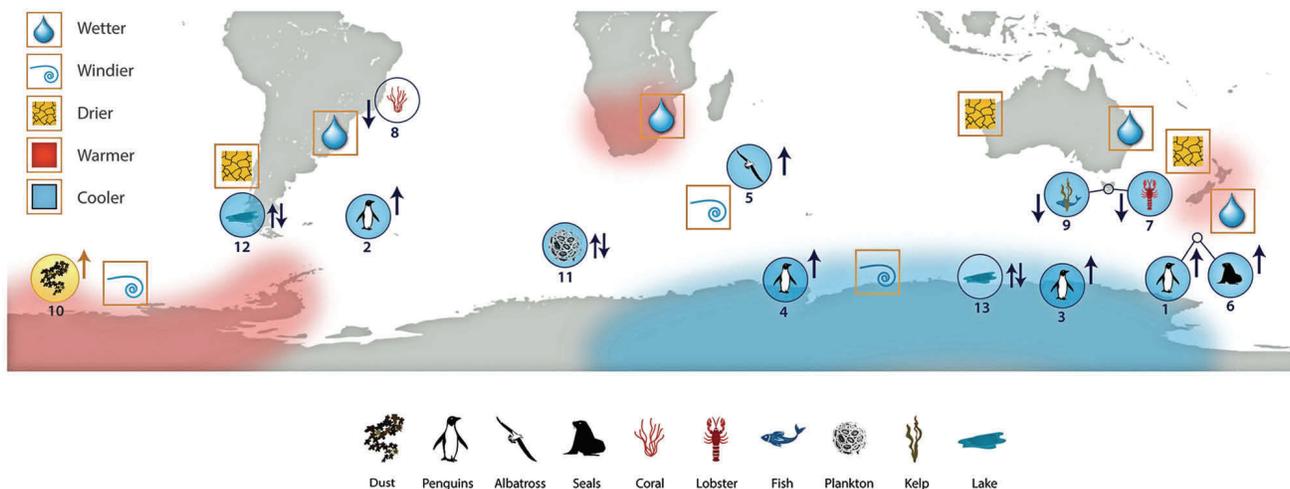
Fig. 10 Map of the southern hemisphere showing how stratospheric ozone depletion affects the climate and environment, and the effects of these abiotic changes on marine ecosystems and populations. Symbols show types of organism, ecosystem or entity affected (see key), with numbers referring to Table 1, which provides location and species details. Arrows indicate direction of effects on biodiversity, up, positive; down, negative effects; two-way arrows indicate changed biodiversity.

Table 1 Summary of how climate change, driven by stratospheric ozone depletion, affects marine ecosystems and populations across the southern hemisphere. Locations (see Fig. 10) and references are provided

Type of ecosystem or organism affected (marker number, Fig. 10)	Species details and biological effects	Location	Ref.
Marine animals			
1	Royal penguins (*Eudyptes schlegeli*); early egg laying	Macquarie Island	234
2	Rockhopper penguins (*Eudyptes chrysocome chrysocome*); positive effects on body mass and reproductive investment in females	Falkland Islands/ Islas Malvinas	235 and 236
3	Emperor penguin (*Aptenodytes forsteri*); juveniles show increased survival	Dumont D'Durville	237
4	Adélie penguins (*Pygoscelis adeliae*); earlier egg laying	Mawson	238
5	Wandering Albatross (*Diomedea exulans*); increased female body mass and better reproductive outcomes	Crozet islands	239–241
6	Elephant seals (*Mirounga leonine*); increased maternal body size	Macquarie Island	242
7	Eastern rock lobsters (*Sagmariasus verreauxi*); distributions shifted south	Tasmania	243
Ocean ecosystems			
8	Corals; declining growth rates	Brazilian coast	244
9	Declines in giant kelp bed extent and fish distributions linked to changing ocean currents	Eastern Tasmania	245
10	Increased transport of dust results in iron fertilisation and could increase productivity of plankton	Southern Ocean	231
11	Changes to the mixed layer depth affect the distribution of both zoo- and phytoplankton, with subsequent consequences for their exposure to UV radiation	Southern Ocean	53
Lake ecosystems			
12	Changes in lake fauna	Eastern side of the Andes	246
13	Lakes becoming more saline causing biodiversity changes	East Antarctic	247

and substantial consequences for populations of foraging sea birds and seals (Fig. 10 and Table 1).[239,241,248] In the sub-Antarctic, the average weight of female wandering albatross is positively associated with the SAM phase, while the age at reproduction is negatively related with the SAM phase. This has led to improved breeding success in recent decades.[239,241] The increasingly positive phase of SAM is also associated with better outcomes for some marine mammals on sub-Antarctic islands. For example, weight of southern elephant seals on Macquarie Island is positively associated with the SAM phase and negatively with the extent of sea-ice.[242]

Across the southern hemisphere, breeding success for four different penguin species (Fig. 10 and Table 1) rose with the increasing positive SAM phase.[234–236,238] Some of these species, such as the Southern rockhopper penguins (*Eudyptes chrysocome chrysocome*), have 'vulnerable' conservation

status.[235,236] Improvements in breeding success are associated with greater weight of adult Southern rockhopper penguins in the sub-Antarctic,[236] and earlier start-date of egg-laying in Royal penguins.[234] In the sea-ice zone near the Antarctic continent, the positive SAM phase is associated with a greater weight of juvenile Emperor penguins and earlier egg-laying date for Adélie penguins.[237,238] These improvements in penguin populations are likely driven by increases in their food supplies in the latitude bands they inhabit, and imply that, by altering the climate, stratospheric ozone depletion results in beneficial effects on some populations of marine birds in certain regions of the Southern Ocean. However, as discussed previously, positive and negative effects of the positive SAM phase on oceanic productivity are likely, and it is not currently known how bird and mammal populations are changing in those areas where productivity is declining (Fig. 10).

Changes in stratospheric ozone depletion and its consequent effects on circulation in oceans could also be altering the distributions of other marine species. For example, recent intensification of the East Australia Current, associated with the positive SAM phase, has shifted the population range of the Eastern rock lobster (*Sagmariasus verreauxi*) southward by *ca.* 270 km.[243] Related to the positive SAM phase, the predicted incursions of warm, nutrient-poor water from the East Australia Current along eastern Tasmania have also increased in strength, duration, and frequency.[245] This has likely contributed to regional declines in the extent of giant kelp beds, as well as to marked changes in the distribution of near-shore fish and octopus, and allowed northern warmer-water species to colonise Tasmanian coastal waters.[245,249] Declines in growth rates in Brazilian corals since the 1970s have also been linked to increasing sea surface temperatures, which were correlated with stratospheric ozone depletion over Antarctica.[244] These findings indicate that there are widespread and far-reaching effects of climate change driven by stratospheric ozone depletion on marine[237] as well as terrestrial[250] (see also ref. 54) ecosystems across the southern hemisphere.[251]

7 Knowledge gaps

Although great advances have been made in recent years in our understanding of the interactive effects of UV radiation and changes in climate and other environmental factors on aquatic ecosystems, major knowledge gaps still exist. Here we assess the most critical remaining knowledge gaps. One of the overarching knowledge gaps is the lack of good data on the spectral dependence of UV radiation effects. All UV radiation effects are highly wavelength dependent, and better weighting functions that quantify the importance of spectral composition of UV radiation, as well as the exposure-response functions, have the potential to substantially improve the accuracy of our estimates of UV radiation effects in nature and the ability to scale results to broader geographic and temporal windows (Fig. 5). Similarly, while experiments with artificial UV lamps can be useful for elucidating some mechanisms of

damage by UV radiation and response, more UV-exposure experiments with natural sunlight and monitoring data, including high resolution UV radiation, are essential to understanding the ultimate overall UV radiation effects on aquatic ecosystems.

Solar disinfection of surface waters of parasites and pathogens is likely one of the most valuable ecosystem services provided by UV radiation: many parasites and pathogens are inactivated by exposure to solar UV radiation.[252] We also know that eutrophication, glacial recession, recovery from acid deposition, and increases in extreme weather events related to climate change are increasing DOM and other UV-absorbing substances in many aquatic ecosystems, potentially reducing this valuable ecosystem service. For example, modeling exposure to UV radiation using the DNA action spectrum (sensitivity of DNA to damage by different UV wavelengths) suggests that higher DOM in many inland waters reduces the solar inactivation potential by up to ten-fold or more in surface waters.[164] What is missing is a direct test of the hypothesised reductions in parasite and pathogen abundance, virulence, and infectivity as a function of DOM concentration and underwater exposure to UV radiation in nature, especially for human parasites. Filling this knowledge gap is key to improving water security and human health as well as to understanding the role of solar UV radiation in controlling parasites and pathogens in aquatic ecosystems.

While we know that exposure to solar UV radiation is damaging to many aquatic organisms at all trophic levels, understanding the net effects of changes in exposure to UV radiation on ecosystems remains elusive. More studies on the simultaneous effects of UV radiation on multiple trophic levels are needed. There remains a substantial challenge to separate out the direct *vs.* indirect effects of UV radiation as well as to separate the adverse effects of short wavelength UV-B radiation from the positive effects of longer wavelengths. For example, longer wavelength UV-A contributes to photosynthesis and primary production, which in turn provide food resources for primary consumers and orientation by zooplankton. UV-B radiation may also have positive effects, since the same short wavelengths of UV-B radiation that cause DNA damage, are also responsible for vitamin D production. Little is known about the role of UV-B radiation in regulating levels of vitamin D in aquatic organisms, although some fatty fish (*e.g.*, salmon) are known to be a good source of vitamin D.[253] Vitamin D is essential to human health and well-being (see ref. 195), and one might speculate it is important to a variety of aquatic organisms as well. While maintaining some low level of exposure of aquatic organisms to solar UV-B radiation may be healthy, almost nothing is known about their requirements for vitamin D or effects of vitamin deficiency. Laboratory experiments on the mechanisms that underlie responses to UV radiation, done under carefully characterised irradiance spectra, may create some advances in our understanding of the contrasting beneficial *vs.* detrimental effects of UV radiation on different trophic levels. Larger scale approaches with wave-

length-selective filters in mesocosms under natural solar radiation, as well as "natural" experiments along environmental gradients in regions of stratospheric ozone depletion, have the greatest potential to create new insights into the underlying mechanisms of response of multiple trophic levels to exposure to UV radiation. These insights into the net effects of UV radiation on aquatic food webs would assist in effective management of water quality, harmful algal blooms, and fisheries productivity, as well as understanding effects on aquatic biodiversity.

Simultaneous changes in climate and other environmental factors interact with the effects of UV radiation, making it difficult to separate out the net effects of UV radiation on observed long-term trends of change in aquatic ecosystems. Inland waters and oceans differ greatly in their size and ecosystem structure as well as the rates and types of environmental change. These differences will have an interactive influence on the effects of UV radiation on any given aquatic ecosystem. For example, increases in atmospheric CO_2 are acidifying the world's oceans as well as some reservoirs and lakes. Yet across major regions of northeastern North America and Northern Europe, pH has increased by as much as a full pH unit related to decreases in anthropogenic acid deposition and increases in extreme precipitation events. These increases in pH are accompanied by up to two-fold or greater decreases in transparency of water to UV radiation in inland waters, and potentially similar changes in coastal estuarine environments. While these largely terrestrially-driven changes will have little effect on open oceans, deposition of dust may interact with nutrients to alter water transparency and effects of UV radiation, even in these vast, nutrient-limited ecosystems. While long-term records show changes in the structure and function of aquatic ecosystems, available data on transparency to UV radiation are too limited to separate the contrasting effects of changes in pH, transparency, and other factors such as nutrients in inland *vs.* marine waters.

Plastic pollution is increasing in aquatic ecosystems, especially in coastal and open oceans (see section 5.2 and ref. 216). UV radiation plays an important role in degrading these plastics, but this degradation produces microplastics and nanoparticles that are taken up into aquatic food webs by zooplankton with unknown fate and effects. Concentrations of microplastics in aquatic food webs pose possible threats to food security, but very little is known about whether these plastics are essentially inert, or toxic to organisms that consume them. Does degradation of plastics by UV radiation lead to a sink that reduces plastic pollution in the environment? Or does it increase their toxicity by enhancing degradation and channeling them into food webs where they threaten food supplies? Phototoxicity, an increase in toxicity of certain compounds such as polycyclic aromatic hydrocarbons when exposed to UV radiation, is well known. But there is little information on the phototoxicity of the products of environmental transformation of other chemicals in aquatic ecosystems.

Finally, assessment of how stratospheric ozone-driven climate changes in the southern hemisphere are affecting bio-

diversity have only just begun and so far, do not yet include many important economic species such as those for fisheries. A better understanding of the proportion that can be attributed to stratospheric ozone depletion would assist with predicting likely future scenarios as the ozone layer recovers.

Filling these knowledge gaps may have important implications for food and water security. Valuable aquatic ecosystem services that are affected by UV radiation range from supplying critical food resources for a major portion of the world's population, to the sequestration of atmospheric carbon dioxide by the oceans and inland waters, to the ability of solar UV radiation to disinfect surface waters of parasites and pathogens, and to the preservation of biodiversity.

8 Conclusions

Stratospheric ozone dynamics and climate change interact strongly with solar UV radiation to control the exposure of aquatic ecosystems to underwater UV radiation, which has both beneficial and detrimental effects on aquatic organisms. The effectiveness of the Montreal Protocol has curtailed the potentially catastrophic high levels of exposure to UV radiation envisioned in the "world avoided" scenario of very high levels of stratospheric ozone depletion. Given the stabilising and recent evidence for recovery of stratospheric ozone, climate change and other environmental variables are now the most important driving factors changing exposure to UV radiation in aquatic ecosystems. In waters of high transparency, UV radiation is still recognised as potentially damaging to organisms at all trophic levels. While most organisms have some level of behavioural avoidance, photoprotection, or photoenzymatic repair that reduces the negative effects of UV, there is still extensive evidence that UV radiation is an important regulator of community structure as well as ecosystem-level processes. For example, incorporating UV photoinhibition into models of primary production in the world's oceans reduces estimates of primary production by about 20%.[75] Reductions in transparency of water related to increases in terrestrially-derived DOM can provide a refuge from damaging UV radiation that enables the survival of UV-sensitive planktonic predators that in turn decimate their prey.[155] In contrast, disinfection of surface waters by UV radiation is a valuable ecosystem service that is being compromised by reductions in transparency of water related to recovery of inland waters from acid deposition, and increases in heavy precipitation that increase inputs of UV-absorbing terrestrial DOM in inland and coastal waters.[164] The use of artificial sunscreens threatens the integrity of aquatic ecosystems near public beaches where concentrations of these toxic compounds are high enough to damage corals, sea urchins, insect larvae, phytoplankton, crustaceans, and fish. Legislation to limit the use of some artificial sunscreens creates new challenges for the cosmetic industry to produce less toxic compounds that are still effective at reducing sunburn and related skin cancers. Ultraviolet radiation breaks down plastic pollutants into microplastics that are ingested by

zooplankton and passed up the foodweb, with unknown effects on food security as these microplastics are found in fish being sold in public markets. Stratospheric ozone depletion is altering the climate in the southern hemisphere with beneficial effects observed in some seabirds, including albatross and penguins, as well as in sea mammals such as seals, but also declines in corals and kelp beds have been reported. This combination of the positive as well as negative effects of UV radiation on aquatic ecosystems and the interactive effects of stratospheric ozone depletion and climate change necessitate continued vigilance and the need to increase our understanding of these complex interactions and consequences for aquatic ecosystems and associated human food and water security.

Conflicts of interest

There are no conflicts to declare.

Acknowledgements

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