Chapter 15

UVR and its effects on species interactions

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Abstract

Species interactions are crucial to understand the control of population growth and community structure. This chapter presents a brief and critical review of what is known about the effects of UVR, (280–400 nm) on species interactions in aquatic ecosystems with emphasis on competition and predation/herbivory. Information on other species interactions such as symbiosis, parasitism, and disease are also briefly reviewed. The existing information indicates that UVR acts as a selective force in pioneer communities of transparent and shallow ecosystems strongly influencing competition output between species at the base of the food web and community structure. However, whether more UV-tolerant species could replace sensitive ones in established communities of natural environments remains uncertain. Examples of positive and negative feedbacks between populations of prey and predators/grazers caused by UVR have been found, but the present information does not ascertain as to whether these mechanisms are widespread in natural ecosystems. Despite the important advance during the last years in our understanding of how ambient and enhanced levels of UV-B radiation (280–320 nm) influence species interactions and trophic relationships, there is still a major gap of knowledge, which is partially attributed to the complexity and biological variability of the species response to UVR, but also to methodological caveats. Consequently, many of the scenarios and hypotheses stated shortly after the discovery of the stratospheric ozone reduction still remain in dispute. Without further research on this topic and the use of more realistic ecological approaches, our assessment of the impact of UVR at the community and ecosystems levels will remain fragmentary and recommendations for sound policy decisions impracticable.

15.1 Introduction

In analyzing the role played by UVR on species interactions, I have included five categories based on the mechanism, namely competition, predation–herbivory, mutualism, parasitism, and disease [1]. The definition and use of these categories in the scientific literature has been flexible as asserted by the interactions between species included under the categories of mutualism, disease, and parasitism [2]. Nevertheless, competition, predation, grazing, and parasitism are among the most important processes in ecology, because they are crucial to understand control mechanisms of population growth and community structure [3].

As we have seen in previous chapters, the bulk of information about the effects of UVR on aquatic organisms has been gathered in studies where species interactions were not considered. Although aquatic ecologists have obtained information on how sensitive different organisms are, including those considered as keystone species, comparatively little effort has been addressed to study potential positive and negative feedbacks caused by UVR on species interactions. Yet, this information is necessary to understand the community and ecosystem response to present and increased levels of incident UVR. Particular-

ly, knowledge at the community level is a pre-requisite for the application of concepts like stability and recovery [4] that has been sometimes wrongly applied in studies of UV impact based on single species.

In general, the characteristics of UVR as an environmental stressor differ from other toxic agents such as pesticides or other man-made chemical substances that were not previously found in environment. As evidenced by the several strategies developed among different forms of life to obtain protection and to repair damage, solar UVR has been an important selective factor during evolution of life on Earth. Moreover, the existence of a temporal pattern in UV irradiances, of a natural vertical gradient of UVR in the water column, of physical refuges, as well as the dual role of UVR (i.e., having negative and positive effects) impart a different nature to the interaction between UVR and aquatic organisms. Although UVR may affect species interactions in a similar way as a toxic substance does, the ecological buffer or adaptive response of aquatic communities to the effects of UVR may well be larger than that to xenobiotics.

Solar UVR may affect species interactions by direct and indirect ways. Figure 1 depicts some examples of hypothetical changes in population size over time of two interacting species with different UV-sensitivity, where the resulting effect has been categorized into neutral, positive, or negative [5]. Despite its simplicity

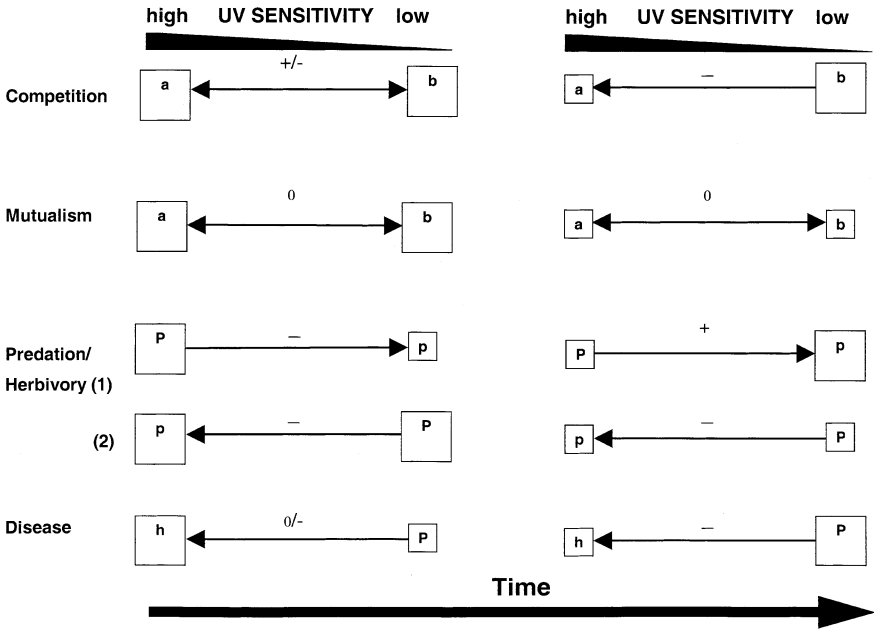

Figure 1. Hypothetical changes in size population over time as affected by differential sensitivity to UVR in five types of species interactions. Size of a population is represented by small or large squares. The 0, +, and − represent the effects of one species on the other (e.g., 0 means a neutral effect of population a on population b). P: predator or parasite, p: prey, and h: host.

and the fact that species interactions are seldom one-to-one in natural food webs, which are usually characterized by a high linkage density (i.e., the average number of interactions per species in the web), Figure 1 provides a framework to analyse the effect of UVR on species interactions and to compare these scenarios with results obtained from the scientific literature.

In this chapter, I shall critically review our knowledge of the link between UVR and the different categories of species interactions mentioned above, trying to lay emphasis on the overall net result in population size for the respective interactions, and, wherever possible, presenting general patterns, identifying major gaps, and future research directions.

15.2 UVR, competition, and changes in species composition

In a pioneering study, Jokiel [6] observed that the UV-tolerant branching sponge *Callyspongia diffusa* replaced the UV-sensitive sponge *Zygomycale parishi* in shallow (<3 m depth) reefs of Kaneohe Bay, Hawaii. He hypothesized that metabolic costs to obtain UV tolerance could place species at a competitive disadvantage in shaded environments, but on the other hand could offer a selective advantage in competition for space in sunlit areas. In a simple and elegant experiment, Jokiel [6] tested whether UV tolerance in *C. diffusa* offers a competitive advantage against *Z. parishi* in the presence of UVR. After 7 days, *Z. parishi* grew over *C. diffusa* in both experimental setups. However, while in the UV-shielded treatment the median tissue overgrowth was 7 mm, it was only 1 mm under full solar radiation. Within 2 months, *Z. parishi* overwhelmed *C. diffusa* in the UV-shielded treatment, but the latter species remained healthy in the UV-exposed one. Although this study did not test wavelength-specific effects of solar UVR on competition, it identified probably for the first time the importance of UVR as an environmental variable potentially affecting species competition in aquatic ecosystems.

One often expected effect of increased levels of incident UV-B radiation in aquatic ecosystems is a change in species composition particularly, of primary producers [7–10]. The rationale behind this hypothesis is based on the different sensitivity to UVR found among species of planktonic and benthic algal communities (see Chapter 11). Changes in species composition within a community are hypothesized to occur by replacement of UV-sensitive species by resistant ones, which occupy similar (trophic) niches [7,9,10]. A change in species composition can take place directly if the population of a UV-sensitive species does not survive to UVR levels above its tolerance threshold or indirectly if outcompeted by more tolerant species. There is strong evidence from several studies in marine and freshwater systems indicating that UVR plays a major role in shaping the structure of communities during the early colonization and succession of many aquatic habitats/ecosystems through selection against less UV-tolerant species [11–18]. However, could enhanced levels of incident UV-B radiation per se lead to the extinction of species in an established (mature) community? Or is it more probable that enhanced (ambient) UV-B levels could cause changes in commu-

nity structure by an alteration in the population size of UV-sensitive and more resistant species as a consequence of different growth rates and competition [19]? Testing the first hypothesis (i.e., extinction) in natural communities is difficult because generally there is a lack of references to what to compare present population/community structure, particularly in places like Antarctica where enhanced UV-B levels have been experienced during the austral spring for more than 20 years. Thus, most studies, except those following a paleo-approach, have tested whether UV-B radiation offers a competitive advantage to tolerant species in long-term micro/mesocosm experiments where UV-B has been excluded and/or artificially enhanced.

Table 1 presents a summary of studies done to test the hypothesis of changes in taxonomic composition in phytoplankton (for which most information is available). The data to address this hypothesis are of uneven quality and the studies differ in experimental design, sophistication level, and statistic strength, so their interpretation in some cases is problematic. Thus, for example, when grazers were present but their abundance was not controlled or their food spectrum not assessed, their effect on changes in phytoplankton species composition will be difficult to discern from those potentially caused by UV-B radiation. Moreover, an additional limitation in the methodology used in exclusion experiments is the distinction between UV-B and UV-A effects. Separation between the effects of these wavebands is generally accomplished by the use of the polyester foil Mylar D (DuPont de Nemours & Co. Inc.). This material, however, cuts off only part of the biologically effective UV-B radiation. For example, when the transmittance of Mylar D (23 μm thickness, 50% transmittance at 316 nm) is multiplied by the solar spectrum for $\sim 40\,^{\circ}$N latitude near summer solstice, it cuts off 60% of UV-B (<320 nm) or only 56% of the biologically effective radiation when the biological weighting function for *Daphnia pulicaria* is used [20]. Furthermore, this value will change depending on the thickness of Mylar D used, which is seldom reported in the experimental design although it strongly affects the cut-off wavelength in the UV-B range.

One of the first studies on this topic was done by Worrest [21] with estuarine phytoplankton (Yaquina Bay, Oregon) exposed in small microcosms (15 L, depth: 0.30 m) to natural solar radiation of wavelengths >380 nm plus enhanced UV-B radiation. The phytoplankton dominated by diatoms changed after 4 weeks (sampling was done only at the beginning and the end of the experiment) with an apparent increase in the dominance of *Chaetoceros* sp. and a decrease of *Skeletonema costatum*. Similar findings have been reported in two studies with phytoplankton from the Gullmar Fjord, Sweden, exposed in small aquaria (18 L and 40 L, depth: 0.23–0.49 m) to artificial UVR or solar radiation plus enhanced UV-B [22,23]. In contrast, in two experiments done in the west coast of Sweden (Gullmar Fjord) with large enclosures (6 m^3, depth: 3.5 m) shifts in phytoplankton species composition were not observed, even in the enhanced UV-B treatments [24]. In microcosm experiments using small containers (1 L) with phytoplankton cultures isolated from Seal Island (Antarctica), changes in taxonomic composition were observed only when exposed to high solar UVR fluxes typical for the tropics, but not under ambient UV irradiances [25]. In another study

Table 1. Summary of studies using microcosms or mesocosms to investigate changes in taxonomic composition of phytoplankton caused by UVR; see text for more details on each study

Habitat	Exposure conditions	Container volume (L)	Duration (d)	Changes	Comments	Reference
Estuarine	solar radiation + enhanced UV-B	15	28	yes	natural assemblage	[21]
Estuarine	artificial UVR	18	7	yes	natural assemblage	[22]
Estuarine	solar radiation + enhanced UV-B	40	10	yes	natural assemblage	[23]
Estuarine	solar radiation + enhanced UV-B	6000	8–11	no	natural assemblage	[24]
Marine	solar radiation	1	5–16	yes	mixed cultures	[25]
Marine	solar radiation	2	15	yes	natural assemblage	[26]
Marine	solar radiation	0.5	8	yes	6 co-occurring species	[27]
Freshwater	solar radiation	1000	16	no	natural assemblage	[29]
Freshwater	solar radiation	300	30	no	natural assemblage	[13]
Freshwater	solar radiation + enhanced UV-B	20000	44	no	natural assemblage	[30]
Freshwater	artificial UVR	600	56	no	natural assemblage	[31]

with surface phytoplankton collected in Arthur Harbor, Antarctica, and exposed to solar radiation in 2 L flasks, important changes in taxonomic composition were observed already after 4 days [26]. In the presence of UVR, the original assemblage composition dominated by flagellates (their experiment #2) shifted by day 13 to the dominance of diatoms. Davidson et al. [27] performed competition experiments in nutrient-rich media using six co-occurring phytoplankton species isolated from the Southern Ocean that were exposed in small bags (0.5 L) to natural solar radiation in an outdoor tank. Their results indicated that overall growth and production by this artificial community was not affected by UVR. However, UV-B caused changes in the growth rate of some species. Thus, for example, growth rate of four diatom species did not change significantly but that of the flagellate stage of *Phaeocystis antarctica* decreased in the presence of UV-B. On the other hand, the growth of the colonial form of *P. antarctica* was enhanced when exposed to UV-B. Changes in species composition were elicited after 2 d exposure and by day 8 the proportion of the colonial form of *P. antarctica* increased mainly at the expense of *Chaetoceros simplex*, although extinction was not observed. These results contrasted with previous studies by Karentz [9] and Karentz and Spero [28] showing that growth of the colonial form of *Phaeocystis* sp. declined in the presence of UV-B radiation. In a field study at the marginal ice zone of the Bellinghausen Sea, *Phaeocystis* populations appeared to be negatively affected by increased levels of UV-B during the "ozone hole", but this did not offer a competitive advantage to co-occurring diatoms species [28].

Results from an experiment with 1 m^3 enclosures (depth: 0.95 m) in a transparent alpine lake from the Austrian Alps indicated no significant differences in species composition after 16 days between the UV-B-shielded and -exposed treatments [29]. Although there were important changes in the proportion of co-occurring species, for example, a decrease in the chrysophyte *Chromulina* sp. and an increase in the chlorophyte *Dyctiosphaerium* sp., the change in dominant species was not caused by UV-B radiation. In another alpine system (Pipit Lake, Canada), no changes in species composition in phytoplankton assemblages, consisting mainly of picocyanobacteria, chrysophytes, cryptophytes, and dinoflagellates, were observed during a 30 days enclosure (0.3 m^3, depth: 0.7 m) experiment where UV-B was excluded [13]. Experiments with large enclosures (20 m^3, depth: 1 m) placed in the littoral zone of mesotrophic Jack's Lake, Canada, showed no evidence for collapse of specific phytoplankton populations or any large-scale taxonomic shift under ambient, UV-B-excluded, or -enhanced treatments [30]. In another long-term experiment (8 weeks) with indoor microcosms (600 L) receiving artificial UVR, no effects of UV-B radiation on species composition, abundance or biovolume of phytoplankton (and other planktonic and benthic communities) was observed [31].

Certainly, a small database as the one presented above may lead to generalizations that are not correct. However, three factors that appear to explain the contrasting results of these studies are the variations in UVR transparency of the water in which the experiments are done, the prior exposure regimes of the species in their place of origin, and the size of the experimental container used in

the studies. The growth rate of phytoplankton species originating from sunlit habitats appears to be less or not at all affected when exposed to UV-B radiation [25,32, see also 33 for a review on other photosynthetic organisms]. Thus, exclusion of UV-B radiation or even its enhancement may not offer a competitive advantage to species already adapted to high solar UV-B irradiances. Beside the obvious disadvantages of the enclosure approach, like, for instance, the elimination of advection and diffusion, the size of the enclosure has a major effect on natural avoidance mechanisms, such as vertical displacement, and on the characteristics of the radiation field experienced by the organisms. Thus, in small-sized enclosures, organisms are exposed to a uniform field of UV radiation due to the short path-length that solar radiation needs to travel before reaching an algal cell [24]. This situation, however, differs largely from natural conditions, particularly in turbid waters (e.g., estuaries) where the water column is characterized by a strong gradient of UV irradiance and spectral characteristics. Together with the absence of mixing that may minimize the UV effect (see Chapter 4) and the long-term (days to weeks) exposure, it is not surprising that significant shifts in species composition caused by UV-B have generally been observed in experiments with small enclosures.

Examples of studies with natural communities of benthic microalgae or with communities of periphyton growing on artificial substrates for long periods are less common. However, in contrast to the dramatic changes observed when pioneer species colonizing new substrates are exposed to UVR, these studies suggest that neither ambient nor enhanced UV-B radiation significantly affects algal species composition [34–37].

Finally, an alternative approach to test the hypothesis of change in species composition has been to look at changes in the dominance of algal species that remain preserved in the sediments, for instance diatoms. In this approach, the main advantage is that the 'historical' reference or initial assemblage structure can be reconstructed in most cases (Chapter 16). On the other hand, it may be difficult to isolate the effect of UVR from other environmental changes, except when recognition of present UV-sensitive species with a long sediment record is possible. Results by McMinn et al. [38] showed that changes during 20 years ($\sim$1971 to 1991) in the relative abundance of diatom taxa analysed in three sediment cores from anoxic basins in Vestfold Hills, Antarctica, were not distinguishable from long-term natural variability. However, as the authors acknowledged, the study was done in a coastal area where a thick ice-cover is present at time of phytoplankton growth and therefore it was not representative of the zone affected by the ozone reduction (see also [39] for other critics on this study). Nevertheless, this approach remains an interesting alternative to explore.

15.3 Herbivory and predation: the complex response of trophic interactions to UVR

In the previous section, the response to UVR of populations at one trophic level (basal species) was considered. The interaction of UVR, however, with more than

one trophic level adds substantial complexity to the possible responses, with the potential occurrence of positive and negative feedbacks (Figure 1). Both prey and predator populations might be affected by UVR, and, if so, the net effect will depend on the relative tolerance threshold of the interacting species. Yet, as soon as we consider more than one interaction between species, responses in the food web are expected to be much more complex than depicted in Figure 1, including potential changes in population size at different trophic levels. Thus, for example, in the hypothetical aquatic food web depicted in Figure 2, a potential reduction in population size of the UV-sensitive species 5 feeding on UV-sensitive basal species 7 and UV-tolerant species 8 and eaten by species 3 may increase the competitive advantage of species 8 and at the same time reduce the population size of species 3 but increase those of 2 and 1.

Bothwell et al. [40] found the first direct evidence of complex interactions in the food web during a colonization experiment with freshwater periphyton growing in artificial flumes of 1 cm depth located outdoor in British Columbia, Canada. They observed that short-term effects of UVR (mainly UV-A) caused inhibition of diatom growth and accrual rate (chlorophyll-*a*). However, after the third week, UVR reduced the number of algal grazers (chironomid larvae mainly *Cricotopus bicinctus* and *Orthocladius* sp.), and by the fourth week, the initial negative effect on algal biomass was reversed. This food web, however, was relatively simple with mainly one herbivore species. Other studies with periphyton in natural streams have failed to confirm the positive feedback described above. For example, in a 28-day study in Otter Creek, Nebraska, ambient levels of UVR did not affect algae or herbivores colonizing tiles submersed at a depth of 8–22 cm [41]. The authors argued that lack of significant differences in herbivore densities between treatments might have been due to the presence of long UV-A wavelengths in the "UV-excluded treatment", which have

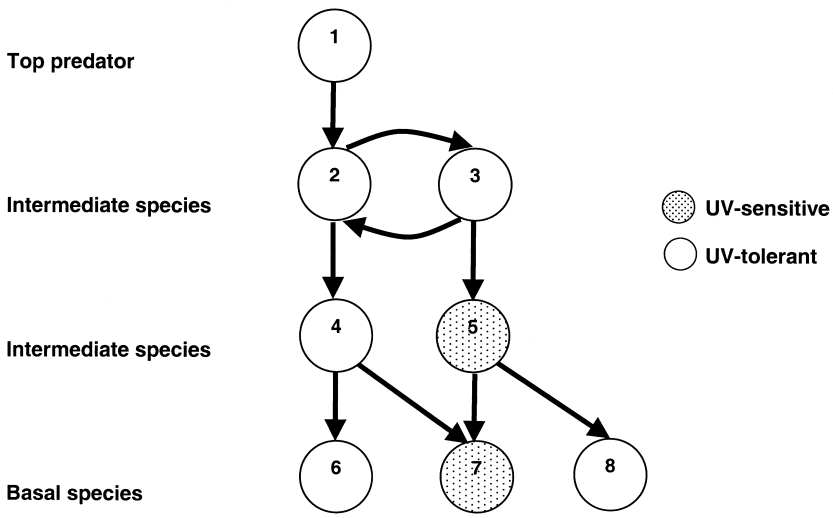

Figure 2. Hypothetical aquatic food web consisting of 8 species having 9 from 64 possible species interactions. [Modified from 2.]

been suggested by Bothwell et al. [40] to elicit UV-avoidance responses of invertebrates. In three colonizing experiments done in the upper White Oak Creek, Tennessee, periphyton and herbivores, mainly the snail *Elimia clavaeformis*, were not significantly affected by ambient UVR levels [42, see also critics and discussions in 43 and 44]. In an experiment lasting 30 days in the Cache la Poudre River, Colorado, a negative effect of UVR on periphyton biomass accrual and abundance of invertebrates colonizing artificial substrates submersed at $\sim$10 to 40 cm depth was only apparent at the end of the experiment [45]. However, the authors concluded that it was unclear whether the effect on invertebrates was caused by UVR, by interaction with other invertebrates, or higher algal biomass in the UV-excluded treatment. They speculated that ending the experiment after 30 days and interrupting successional shifts in algal species might have avoided a positive feedback of UVR on algal biomass. McNamara and Hill [36] suggested that the different responses of periphyton observed in the studies mentioned above are related to the presence of more UV-resistant communities in streams at low elevations of mid-latitudes than at higher elevation or latitudes. This seems to be counterintuitive because UV-B fluxes increase with altitude (see Chapter 2). On the other hand, several authors have argued that one possible explanation for the dissimilar results obtained are the different exposure characteristics of organisms in artificial flumes and natural streams, particularly the shallow depth and exclusion of higher-level predators that may exacerbate the effects of UVR on periphyton and insect larvae [15,41,45].

A lack of indirect effects mediated by UVR has also been observed in a colonizing experiment in an alpine lake [13]. While development of epilithon (mainly diatoms and cryptophytes) was suppressed by UV-A and UV-B radiation, zoobenthos like the sediment-dwelling *Gammarus lacustris* and chironomids with burrowing habits were not affected. There are only a few studies in coastal marine environments addressing this topic. During an experiment in the coast of Greece, biomass of colonizing benthic algae (mainly pennate diatoms) and species community structure were affected by ambient levels of UV-B, but invertebrate biomass was not [15].

Autecological studies with freshwater and marine heterotrophic nanoflagellates (HNF) have provided some evidence for a positive feedback between UVR and prey populations. Sommaruga et al. [46] reported that artificial and natural UVR (mainly UV-B but also UV-A) strongly reduced bacterivory rates of the freshwater HNF *Bodo saltans*. In laboratory experiments, they found that mortality rates (i.e., negative growth rates) of bacteria in the UV-B-excluded or dark treatments were higher than in the presence of UV-B. Furthermore, depending on predator density, even positive bacterial growth rates were observed in the presence of UV-B [46]. Similar evidence was obtained by Ochs [47,48] in laboratory experiments with the marine HNF *Paraphysomonas bandaiensis* and *P. imperforata* grazing on two strains of the picocyanobacterium *Synechococcus* sp. Prey population size was always higher in those treatments where grazing by HNF was more affected by UVR. On the other hand, studies with natural protist assemblages exposed to ambient and enhanced UV-B levels have provided

mixed results. In a study with microbial communities from two arctic systems, although ambient UV-B levels negatively affected growth of some ciliates species, community-grazing rates were not [49]. In a 16-day mesocosm experiment with a microbial food web (zooplankton excluded) from a UV-transparent alpine lake, negative effects of ambient UV-B radiation were observed on HNF growth and bacterivory rates. However, this did not result in higher bacterial abundance suggesting that bacteria were negatively affected as well [50]. In an experiment with a microbial food web (organisms $>240\ \mu$m excluded) from the St. Lawrence Estuary, Canada, enhanced UV-B radiation reduced significantly the populations of large phytoplankton and ciliates after 7 days [51]. The increase in prey abundance, mainly in HNF, was interpreted as a release from predation pressure by ciliates [52]. Reductions in HNF bacterivory rates were not observed until the 7th day [53] when bacterial abundance increased [54]. In other two mesocosm studies with estuarine communities (including zooplankton), no major effects to enhanced UV-B levels were observed except for phytoplankton in one of the studies, while positive feedbacks among different components including fish larvae were not found [55,56].

Another potential effect of UVR on the predator–prey interaction is when the prey population has a higher UV-sensitivity than the predator, potentially leading to a negative feedback (Figure 1 case 2 of predation/herbivory). Investigations on this possible scenario have been based on the observation that the UV-B-irradiated green alga *Selenastrum capricornutum* was ingested by *Daphnia magna* but digested with lower efficiency than those in the control without UV-B [57]. This effect was significant only after ≥ 12 h irradiation with artificial UV-B radiation (max. at 312 nm). The authors hypothesized that changes in both mucous secretion and in thickness of the cell wall were responsible for the lower digestibility. In a later study, other species of phytoplankton (*Chlamydomonas reinhardtii*, *Scenedesmus acutus*, *S. subspicatus*, and *Cryptomonas pyrenoidifera*) cultured in the presence of a high UV-B dose were assessed for qualitative and quantitative cell changes and their effect on life-history parameters of *D. pulex* [58]. Beside reduction of algal growth rates by UV-B, important changes in the nutritional quality of the algae (e.g., total lipid concentration and fatty acids composition) were also observed. The intrinsic growth rate of *D. pulex* kept in the dark, however, was only significantly affected when feeding on the UV-irradiated *S. subspicatus*. Changes in intrinsic growth rate were mainly caused by a smaller number of offspring in the UV-B treatment. On the other hand, UV-B-irradiated *C. reinhardtii* and *C. pyrenoidifera* caused a reduction in the length of newborns in the first clutch. Changes in survival of *D. pulex* were not observed in all cases. Interestingly, in a similar experiment, but including another culture strain of *C. reinhardtii*, the survival of *D. pulex* neonates kept in the dark was strongly affected when feeding on UV-B-irradiated algae [59]. *Daphnia* feeding on UV-B-irradiated algae also showed reduced intrinsic growth rates, clutch number and size. In this experiment, the growth rate of *C. reinhardtii* was only affected at the beginning but after 7 days it was similar to the control and changes in total lipids concentration were not observed. The results of these studies, although interesting, are difficult to interpret with regard to the net response of changes in

population size. Whereas species of *Daphnia* like *D. magna* are known to be UV-B-sensitive [60,61], additional parallel experiments with *D. magna* and *D. pulex* concomitantly exposed to UVR would have been necessary to evaluate this interaction. On the other hand, the contrasting results obtained using the same species but different strains [58,59] stress the large biological variability found in response to the exposure to UVR.

In the only one study with freshwater periphyton, enhanced UV-B levels reduced photosynthesis and photosynthetic pigments, but algal nutritional quality (as measured by cell N and P content) and growth of juveniles of the snail *Physella gyrina* fed with UV-B-irradiated periphyton were not altered [36].

15.4 Mutualism and UVR: symbiosis of algae-invertebrates and algae-protists

Most of our knowledge on the interaction between UVR and mutualistic associations is based on studies on algal-invertebrate symbiosis, particularly on scleractinian corals and their endosymbiotic dinoflagellates, the so-called zooxanthellae from the genus *Symbiodinium*. Recently, the scientific literature on this topic has been extensively reviewed [33,62,63]. Here, I will only briefly highlight the most important aspects regarding potential population changes in this association as affected by UVR and review the information for other symbiotic relationships.

Bleaching or discoloration in corals has increased dramatically in tropical areas over the past 20 years. This phenomenon is the result of the expulsion or loss of endosymbionts or at least their pigments. Although not necessarily lethal to the coral, widespread bleaching may cause massive death of coral reefs [64,65]. The role of solar UVR as responsible for coral bleaching remains controversial [33]. However, independently of the factor(s) that may cause bleaching, expulsion of endosymbiotic zooxanthellae will expose them directly to the potential negative effects of UVR. Several studies have shown that UVR inhibits the growth of different species of *Symbiodinium* when isolated from the host, although species-specific differences in sensitivity have also been observed [33]. Furthermore, UVR severely depresses photosynthetic rates in freshly isolated zooxanthellae from corals or other reef organisms, but this effect is small or absent *in hospite*. For example, in *Prochloron* sp., a prokaryotic microalgal symbiont of a colonial tropical ascidia, photosynthesis was strongly inhibited in isolation but not in the host [66]. The different sensitivity between isolated and *in hospite* forms appears to be related to protection given by the host through the accumulation in their tissue of sunscreens such as mycosporine-like amino acids (see Chapter 10).

Symbiosis between algae and protists is widespread, for example, among marine and freshwater planktonic ciliates and larger foraminifera. In some cases, the whole cell of different groups of algae lives as endosymbionts in the host, while other species preserve only the plastids. Although the latter type of association is not a "true symbiosis", functionally, plastids represent a source of

photosynthetic products for the host, similarly to true algal endosymbionts [67]. Surprisingly, effects of UVR on algal–protozoan symbiotic associations have hardly been studied despite their important role in food webs, particularly as primary producers in oligotrophic systems. Martin-Webb [68] performed UV-exclusion experiments with natural ciliate assemblages including *Mesodinium rubrum* and *Laboea strobila* collected from a shallow area (Georg Bank, 40–42 °N) on the continental shelf, NW Atlantic. The haptorid ciliate *M. rubrum* contains a cryptophyte symbiont and is an important primary producer in coastal areas [69], while the large-sized *L. strobila* is a conspicuous plastidic oligotrichid in temperate waters [70]. Results from these experiments indicated a lower UV-B sensitivity in symbiotic than other ciliates from this coastal area [68].

Large foraminifera from several families have endosymbionts represented by chlorophytes, rhodophytes, dinoflagellates, or pennate diatoms. The type of algal symbionts appears to influence the optimal depth occupied by some species of foraminifera [71]. Yet, bleaching, particularly of the reef-dwelling *Amphistegina gibbosa*, has been observed in populations of subtropical waters like the Florida Keys [72]. Indirect evidence suggests that, similar to bleaching in corals, UVR may be contributing to this phenomenon [72,73]. Thus, for example, *A. gibbosa* shows a seasonal bleaching cycle with maxima during the summer solstices, preceding maximum summer water temperature by *ca.* two months. Moreover, bleaching in this species is observed in remote areas, where pollution is unlikely to be a contributing factor [72,73]. Interestingly, affected *A. gibbosa* is highly predated by the foraminifer *Floresina amphiphaga* and also often found infested by cyanobacteria. These observations were never recorded before the detection of bleaching in this species [73].

15.5 The interaction between UVR and parasites

This type of interaction is obviously restricted to ectoparasites or to the free stadium of endoparasites. Although UVR is generally associated with negative effects, it may also play a positive role on species interactions. Thus, for example, the ectoparasite copepod *Lepeophtheirus salmonis* (salmon lice) uses photoreceptors to avoid UVR and eventually to optimise host finding (e.g., by utilizing UV contrast vision [74]).

Most of our knowledge on the interaction between UVR and parasites, however, is related to viruses, which, although considered obligatory parasites, resemble a predator–prey interaction [75]. Due to the obligatory use of the host metabolic machinery to produce new viral copies and the impossibility to repair themselves, viruses are very vulnerable to several stressors when occurring in the water column. Among other environmental factors, solar UVR affects viruses negatively by reducing their infectivity [76]. Loss of viral infectivity after exposure to solar radiation seems to be mainly caused by damage to the viral genome, although indirect damage to the capsid has also been suggested to result in inactivation [77]. Wavelengths < 320 nm are generally the most effective ones to

cause viral inactivation [78], although UV-A radiation [79] and wavelengths <556 nm [77] have been found to inactivate viruses as well. Like in many other planktonic groups, different viruses appear to have different tolerance towards solar radiation [77,78,80], but the reason(s) for this remains unclear. Kellogg and Paul [81] found that the degree of UV damage of six marine vibriophages was negatively correlated with the G+C content and suggested that the increase of thymine dimer targets increases their sensitivity by reducing the ability to repair the damage, a hypothesis previously proposed for bacteria by Singer and Ames [82]. The DNA damage, however, can be repaired after infection takes place using the host repair mechanisms. Thus, different repair mechanisms or efficiencies may also explain the variability observed in virus inactivation rates. The infectivity of phages can be restored inside bacteria, either through a specific host-repair-machinery (=photoreactivation) [83,84] or by a virus encoded repair system [85,86]. The light-dependent repair mechanism of bacteria seems to be crucial to restore the infectivity of natural aquatic viruses [83,84,87]. Therefore, the potential recovery of viruses makes it difficult to predict the overall effect of UVR in this interaction. Moreover, the inactivation–recovery process is further complicated by the fact that the physiological status of bacteria can be also impaired by UVR [88,89, see also Chapter 13].

The physical disruption/destruction of the viral particle by high-energy photons is another mechanism that can account for loss of viral abundance [90]. The exact mechanism of this destruction, however, is not well understood and the experimental results gathered with different viruses are inconclusive [91,92].

Finally, another potential interplay between UVR and viruses occurs when they coexist with their host in a type of mutualistic relationship, where the nucleic acid of the virus is integrated in the genome of the host and is replicated with it (lysogenic state). Ultraviolet C radiation produced by germicidal lamps (max. at ~ 254 nm) has normally been used, among other stressors, to induce the shift from lysogenic to lytic state in a complex mechanism involving the DNA repair SOS system of the host [93]. However, natural or simulated solar UVR seems not to be very efficient in this process [94,95].

15.6 UV radiation and infection diseases

Parasitism is an important ecological interaction that may cause dramatic changes in the host population size. As discussed above, solar UVR has the potential to act directly or indirectly in this process, for example by damaging the parasite or by causing damage to the host and increasing its susceptibility to infections. About the latter type of interaction, our knowledge is restricted mainly to studies on fish and amphibians. Solar UV-B radiation is known to cause injury to the skin (sunburn), reduction of goblet cells (mucus secreting cells), and epidermal hyperplasia in fish although sensitivity is species- and developmental stage-specific [96,97]. The damaged skin tissue is usually susceptible to bacterial and parasite infections. Particularly, *Saprolegnia*, an oomycete, is a common opportunistic facultative parasite of freshwater fish [96]. Infection

by *Saprolegnia* causes loss of epithelial integrity and tissue destruction due to cellular necrosis or dermal and epidermal damage [98,99]. Infections may result from direct UV-B damage to the skin or from suppression of the immune system. In the case of the parasite *Saprolegnia*, the decrease in the secretion of mucus appears to be crucial for the infection as it acts as the primary physical barrier [100]. However, UV-B radiation may have a strong immunosuppressive effect on fish, probably weakening their resistance to infectious agents in relation to impairment of the non-specific immune defense [101]. Nevertheless, secondary parasitic infections by *Saprolegnia* after UV-B exposure appear to have been only documented for laboratory studies [102]. On the other hand, results from field observations and experiments have shown that increased UV-B exposure of western toads embryo, *Bufo boreas* caused by reduction in water depth at oviposition sites are related to higher infection by *S. ferax* [103,104]. For example, *S. ferax*-associated mortality (i.e. the proportion of dead to hatching embryos) was higher than 50% at water depths <20 cm depth but less than 19% in water deeper than 45 cm [104].

15.7 Summary and concluding remarks

Taken together, the results presented in section 15.2 suggest that the extinction of entire populations of basal species by enhanced UV-B levels seems improbable in established aquatic communities. In transparent and shallow aquatic ecosystems, UVR is undoubtedly a major force shaping the structure of pioneer communities. However, whether enhanced UV-B fluxes could offer a competitive advantage to tolerant species of phytoplankton in natural environments remains uncertain. A major effort is needed to understand the underlying physiological mechanisms resulting in the observed changes or lack of changes in community structure. Although there is probably no perfect experimental design to test the direct and indirect effects of UVR, ecological studies should resemble the conditions to which organisms are exposed to solar radiation. The contrasting results obtained with enclosure experiments and the highlighted methodological caveats call for extreme caution in extrapolating previous results on changes in species composition to natural environments. In connection to scenarios of shift in taxonomic composition, it has often been anticipated that a change in phytoplankton (or other community) species composition will have a major impact on higher trophic levels and cause altered patterns of trophic dynamics [7,8,105]. This Eltonian perspective of ecosystem functioning may not necessarily apply even under the worst-case scenario of population extinction. Analyses of food web studies where species have been removed, and predictions of the food-web theory, suggest that consequences for higher trophic levels will depend on both the functioning role of the species (e.g., a keystone species) and the complexity of the food web [106]. Thus, for example, the extinction of a species in a simple food web with few dominant species may have dramatic consequences for higher trophic levels (resulting potentially in other extinctions), while in a complex community the effects will be small. These predictions are further supported by

the observation that linkage density in food webs increases with their size [107], and that regardless of the size of the food web there is a nearly constant ratio (~ 2 to 3) of prey to each predator species [108].

The existing information about indirect effects mediated by UVR on trophic interactions (section 15.3) suggest that positive feedbacks as observed in artificial flumes with benthic organisms and in laboratory studies with microorganisms are not the rule in natural systems. Certainly, more ecological studies are needed before we can consider them as important processes occurring in aquatic ecosystems. Particularly, a combination of autecological and synecological approaches could be fruitful in view of the large difference in species sensitivity observed. Assessments where entire components are considered as "black boxes" will mask the species' response. On the other hand, it can be anticipated that for planktonic groups with uncertain or difficult taxonomy this would be a difficult task. Regarding indirect effects of UVR on grazers mediated through algae, there is an urgent need to do experiments under more realistic UV exposure conditions considering the combined effect of UVR on grazers. A less explored interaction is when UVR acts together with predation as countervailing selective pressure on aquatic organisms that obtain protection through pigmentation but at the same time increase their conspicuousness to predators [109,110]. The effect of UVR on food quality, particularly on polyunsaturated fatty acids are thought to play a major role in the food web of shallow and clear waters as these compounds are essential for a balanced growth in herbivores [111].†font COLOR = '£ff0000'· Consequently, studies considering the effect of changes in food quality and life history traits of invertebrates as affected by UVR are a promising research line. Finally, the effects of UVR on anti-predator behavioural responses as evidenced for amphibians [112] need to be investigated on different groups of organisms including the direct effect of UVR on chemical signals (e.g. kairomones) important in predator–prey relationships.

Although there is an increasing number of studies addressing the role of UVR on the mortality of symbiotic corals, our knowledge of UV effects on other types of symbioses in marine and freshwater systems is scarce (section 15.4). It seems reasonable to hypothesize that beside the well-established advantage of endosymbiosis for survival in nutrient-poor waters, symbionts, for instance, of protozoans, may also offer protection against UV damage by providing photoprotecting compounds such as mycosporine-like amino acids. The finding that symbiotic ciliates are less UV-sensitive than other ciliate species supports such assumptions. The study of the association between phototrophic endosymbionts and ciliates living in the illuminated zone of anoxic marine sandy sediments could be particularly interesting in this regard.

Information on the effects of UVR on parasites and diseases in aquatic systems is mainly restricted to viruses and *Saprolegnia* spp. As we have seen in section 15.5, the interaction among UVR, viruses, and their hosts is extremely complex including direct and indirect effects. The use of models may help to explore the response of this system under UV stress. For example, the time needed to intercept a host depends on the product of contact rate, host population, and the inverse probability of infection per contact [90]. Results from a random encoun-

ter model predict that viruses of common (abundant) species may have an advantage by requiring less time to contact their host and consequently by receiving a lower UV dose in exposed habitats [113]. Consequently, viruses from bacteria should be less exposed to damaging UV irradiances than those of phytoplankton. However, host specificity may reduce the effective population size that could be infected. Obviously, this is a field where more research is needed to define the net response of the interaction.

The example of *Saprolegnia*-associated mortality on amphibians represents a good example of how other synergistic processes, like climatic warming may exacerbate negative effects of ambient UVR (see Chapter 17). Whereas secondary parasitic infection by *Saprolegnia* after UV exposure seems to be more common in captive fish, this parasite is responsible for a high mortality in natural populations of amphibians. Nevertheless, it remains to be established how sensitively *Saprolegnia* species react to increased UV-B fluxes.

This brief review clearly indicates that ecologists still have much to learn about the interactions of UVR in the functioning of aquatic ecosystems and, at the same time, much to contribute to this topic. Although it is obvious that the role of UVR on species interactions is now recognized by aquatic ecologists and considered essential for assessing the ecosystem response, our gap of knowledge is still large. One consequence of this situation is that many predictions about potential effects of enhanced UV-B fluxes on aquatic ecosystems remain only speculations. This must change rapidly in the near future, considering that scientific knowledge alone does not lead to political decisions, and that policy based on a weak scientific basis is doomed [2].

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