Photochemistry and Photobiology, 2006, 82: 850–856

Symposium-in-Print: UV Effects on Aquatic and Coastal Ecosystems

UV Effects on Marine Planktonic Food Webs: A Synthesis of Results from Mesocosm Studies

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Received 27 September 2005; accepted 21 March 2006; published online 23 March 2006 DOI: 10.1562/2005-09-27-RA-699

ABSTRACT

UV irradiance has a broad range of effects on marine planktonic organisms. Direct and indirect effects on individual organisms have complex impacts on food-web structure and dynamics, with implications for carbon and nutrient cycling. Mesocosm experiments are well suited for the study of such complex interrelationships. Mesocosms offer the possibility to conduct well-controlled experiments with intact planktonic communities in physical, chemical and light conditions mimicking those of the natural environment. In allowing the manipulation of UV intensities and light spectral composition, the experimental mesocosm approach has proven to be especially useful in assessing the impacts at the community level. This review of mesocosm studies shows that, although a UV increase even well above natural intensities often has subtle effects on bulk biomass (carbon and chlorophyll), it can significantly impact the food-web structure because of different sensitivity to UV among planktonic organisms. Given the complexity of UV impacts, as evidenced by results of mesocosm studies, interactions between UV and changing environmental conditions (*e.g.* eutrophication and climate change) are likely to have significant effects on the function of marine ecosystems.

INTRODUCTION

The human-induced destruction of the stratospheric ozone layer and the resulting increase of UV-B irradiance (280–320 nm) since the late 1970s stimulated research on the effects of UV-B on biological systems. UV-B can produce significant effects, including optical and photochemical changes, at all levels of aquatic ecosystems (1–3). Although UV-A irradiance (320–400 nm) is not affected by stratospheric ozone destruction, it penetrates deeper in the water column than UV-B and it is responsible for a large part of the overall UV-associated photochemical and photobiological effects in aquatic environments. Moreover, changes in the ratio between UV-B, UV-A and photosynthetically available radiation (PAR; 400–700 nm) can affect photorepair and photoacclimation mechanisms (4,5).

Most of our understanding of the effects of UV on individual organisms and physiological processes in the aquatic environment has been obtained from laboratory experiments, in which a high degree of control can be achieved but complex ecological interactions are difficult to reproduce. Field studies have also greatly contributed to the study of UV impacts although conditions for hypothesis testing are not often encountered in coastal, estuarine and pelagic systems. In these highly dynamic environments, multiple stressors are at play and complex ecological relationships may blur the signal associated with the impact of UV. Owing to the possibility of achieving a good balance among control, realism and generality (6,7), mesocosms are well suited for the study of the impact of UV on plankton communities.

Mesocosms, defined as large outdoor enclosures (volume, >1 m^3), have proven to be useful tools in the study of structure and function of the aquatic ecosystems and have provided insights into the impact of environmental changes on freshwater and marine ecosystems. Similar to all other experimental approaches, the analysis of mesocosms has limitations, with scaling problems often identified as the most important (Carpenter (8)). However, such enclosures enable controlled, manipulative experiments for the study of community-level processes that would be otherwise difficult or impossible to investigate in the laboratory or *in situ* (9,10).

In this review a synthesis of the findings of mesocosms studies of the impact of UV on marine planktonic organisms is presented. The

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Table 1. Mesocosm experiments considered in this review.*

Exp no.	References	Mesocosm volume (L)	Mesocosm depth (m)	Mesocosms walls	Experiment duration (days)	Mixing	Trophic levels studied	Treatments
1	Keller *et al.* (11)	13000	5	Opaque (white)	70	Yes (paddles)	Phyto Zoo Fish	Natural +UV
2	Keller *et al.* (12)	13000	5	Opaque (white)	30	No (stratified)	Phyto μzoo Zoo Fish	Natural +UV
3	Belzile *et al.* (19) Mostajir *et al.* (27) Mostajir *et al.* (32) Chatila *et al.* (33) Chatila *et al.* (48) Fauchot *et al.* (26) Mousseau *et al.* (49)	1500	2.25	Opaque (stainless steel)	7	Yes (pump)	Bact Phyto μzoo	Natural −UV +UV ++UV
4	Wängberg *et al.* (28) Gustavson *et al.* (50)	6185	3.5	Clear polyethylene	11	No	Bact Phyto	Natural −UV +UV
5	Wängberg *et al.* (28)	6185	3.5	Clear polyethylene	8	No	Phyto	Natural −UV +UV ++UV
6	Gustavson *et al.* (50)	6185	3.5	Clear polyethylene	6	No	Bact	Natural −UV +UV
7	Whitehead *et al.* (25) Fouilland *et al.* (23)	1500	2.25	Opaque (stainless steel)	10	Yes (pump)	Bacteria Phyto	Natural +UV
8	Bouchard *et al.* (14) Longhi *et al.* (15)	2000	2.3	Clear polyethylene	10	Yes (pump)	Phyto	Natural +UV
9	Bouchard *et al.* (14) Longhi *et al.* (15)	1800	1.9	Clear polyethylene	7	Yes (pump)	Phyto	Natural +UV
10	Bouchard *et al.* (14) Longhi *et al.* (15)	1900	2.4	Clear polyethylene	10	Yes (pump)	Phyto	Natural +UV

*The experiments are ordered by the date of publication. The analysis is restricted to studies using marine/estuarine enclosed experimental ecosystems with volume larger than 1 m^3. Trophic levels: Bact = bacteria, Phyto = phytoplankton, μzoo = microzooplankton, zoo = macrozooplankton.

analysis was restricted to studies of mesocosms with a volume >1 m^3 so that comparable variations in the relationship between light and depth and similar ecosystem trophic complexity could be considered. On the basis of results of an exhaustive literature search, a total of 10 experiments presented in 15 different articles are synthesized (Table 1). First, emphasis is put on the different experimental setups that have been developed. Second, a brief overview of UV impacts on autotrophs, bacteria, heterotrophic protists and zooplankton is presented. Third, observed impacts on planktonic food web and community structure are synthesized. Finally, we identify some gaps in the understanding of UV impacts and suggest future research avenues.

SETUP CONSIDERATIONS

Manipulation of UV irradiance in mesocosm experiments

One of the most useful aspects of mesocosms in UV research is that they enable manipulation of the light field by use of lamps and selective screens. For instance, the use of Mylar film to block incident UV-B has been widespread in field experiments involving bottle incubations and was also part of the experimental setup of numerous mesocosms studies (–UV treatment; Table 1). These UV-exclusion experiments have shown that natural levels of UV affect multiple trophic levels in the plankton. The natural levels of UV also impact dissolved organic matter cycling through photodegradation and the UV-induced photobleaching of DOM increases the water transparency to UV. Despite the useful insights into photochemistry and photobiology gained from UV-exclusion experiments, the impact of the increase in UV above natural levels (as results from ozone depletion) is best studied by supplementing natural sunlight with UV lamps (+UV treatments; Table 1). The UV intensity and daily exposure can be adjusted by varying the number of lamps, the distance between the lamps and the water surface and the duration the lamps are on each day. Most mesocosm studies have used a step function in which the UV increase is a square-wave increase (the lamps are simply turned on in the morning and turned off in the afternoon). However, a few experiments have tried to achieve UV intensities proportional to PAR (11,12). Although this latter approach is preferable to a square-wave increase, it should be noted that assigning a constant ratio between UV and PAR is also not a fully realistic approach, because the ratio of UV to PAR varies greatly during the day under natural conditions (the ratio of UV to PAR is higher at noon). Computer-modulated systems that increase UV-B as a function of ambient UV were developed and used successfully for small-scale experiments (*i.e.* 40 L aquaria (13)) and mesocosm studies (14,15).

When selecting a lamp for UV increase care should be taken to achieve a spectral quality that resembles that of natural sunlight. Because ozone depletion only affects UV-B irradiance, UV-A emission by the chosen lamps should be minimal. Most importantly, the shorter UV wavelengths that do not occur in nature but are emitted by the lamps (*i.e.* <280 or 290 nm) must be removed by

the use of cellulose acetate film. Because cellulose acetate film is subject to aging (it becomes more opaque with time), its spectral transmission should be monitored to avoid any significant decrease in UV supplement over the course of the experiment (16).

Although care is generally taken to ensure a good characterization of the spectral UV enhancement, it is equally important to accurately measure the irradiance attenuation in the water column inside the mesocosms. When using opaque-walled mesocosms the irradiance attenuation within the mesocosms is much greater than would be predicted from the optically active components in the water column (*i.e.* the water molecules, colored dissolved substances, phytoplankton cells and nonalgal particles) (17,18). This increased attenuation is due to absorption of the photons by the mesocosm walls and the increased path length resulting from reflection on the walls. White walls can be used to maximize the reflection of sunlight, somewhat counterbalancing the shading effects associated with opaque walls (11,12). When transparent mesocosms immersed in water are used irradiance attenuation should approximate that of the natural environment as long as the water inside and water outside the mesocosms have approximately the same optical properties. Shading effects caused by structures surrounding the mesocosms and by the UV lamps over them should be minimized and their impact on the underwater light field quantified (19). The increased attenuation caused by wall effects and shading effects is crucially important because it decreases the UV irradiance integrated over the water column to a level lower than would occur in the natural environment. This may partly explain why relatively high UV increases sometimes have little impact on plankton enclosed in mesocosms.

The integrated irradiance (or cumulative exposure) can be calculated as the daily irradiance averaged over the water column, $\bar{E}_d(\lambda)$:

$$\bar{E}_d(\lambda) = [E_d(0^-, \lambda)(1 - \exp(-K_d(\lambda)z)]/(K_d(\lambda)z) \qquad \text{(Eq. 1)}$$

where $E_d(0^-, \lambda)$ is the downwelling irradiance just below the water surface at wavelength λ, $K_d(\lambda)$ is the diffuse attenuation coefficient for E_d and z is the water depth (19,20). Although this and similar formulations are widely used in photobiology, a more appropriate approach would include partitioning the irradiance absorption according to the organisms of interest relative to that of the whole suite of optically active substances. For example, a given $\bar{E}_d(\lambda)$ in a system with high colored dissolved organic matter (CDOM) absorption would likely have a much smaller impact on phytoplankton photosynthesis than a system with low CDOM absorption, because in the first case most UV photons are actually absorbed by CDOM rather than phytoplankton.

Because shorter wavelengths in the UV generally have the larger impact on biological and photochemical processes, it is generally more appropriate to weight the spectral UV irradiance by a biological weighting factor (BWF; similar to the apparent quantum yield of photochemistry [21]). One current limitation is that BWFs are more or less specific to certain physiological processes at certain times and locations and are therefore difficult to generalize and apply to ecosystem-level studies. Because the more biologically effective wavelengths are also the most rapidly attenuated, the attenuation of UV in the water column of mesocosms is especially important to asses and quantify.

Simulation of vertical mixing and turbulence

In marine environments as well as mesocosms enclosures irradiance decreases approximately exponentially with depth. The exposure to UV is therefore a direct function of the position and residence time of the planktonic organisms within the photoactive zone, as dictated by stratification and mixing; this photoactive zone is often considered to be the zone between the surface and the depth where 10% of surface UV-B irradiance remains (22). Most of the UV mesocosms studies have used pumps or rotating paddles to insure a complete mixing of the water column (Table 1). One notable exception is the work of Keller *et al.* (12), in which chilling of the bottom water to 3–5°C below the surface temperature created stratification within the mesocosms. In 2.25 m deep mesocosms a flow rate that passed the entire volume of the mesocosm (1500 L) through the circulating pump every 3 h was shown to be sufficient to create homogenous vertical distribution of nutrients and particulate matter (23). A well-mixed water column insures that a sample taken at any depth is representative of the whole water column, thus decreasing the sampling effort (although processes with time scale smaller than *ca* 1 h can still show vertical variations).

Because the photoactive zone in the natural environment is generally shallower than the upper mixed zone, vertical mixing exposes organisms and molecules alternatively to high and low UV intensities. The depth of the upper mixed layer influences the average UV exposure and the rate of vertical transport determines the residence time in and out the photoactive zone (22). The kinetics of UV damage and recovery are the most important factors determining the effect of vertical mixing on UV impact. If all biological and chemical effects were linear functions of cumulative exposure over all time scales, then the timing and sequence of exposure as dictated by vertical mixing would not matter (22). However, UV effects are often not proportional to the cumulative exposure but depend on irradiance level and exposure duration; that is, reciprocity fails (21,22,24). In other words, for a given cumulative exposure a short duration of exposure to high UV irradiance does not have the same effect as a long duration of exposure to lower irradiance. Mixing also affects acclimation to UV because the relatively high PAR and UV irradiance generally associated with a shallow mixed layer favors the establishment of protective mechanisms (*e.g.* accessory pigments and mycosporine-like amino acids) and defensive mechanisms (*e.g.* repair) (5). In the less frequent situation, in which the mixed layer is shallower than the photoactive zone (*e.g.* during formation of diurnal stratification), mixing is likely to decrease depth-averaged UV effects because already damaged plankton shields the deeper populations and these deep populations still have access to light for photosynthesis and often also access to nutrients.

The mesocosm experiment described by Whitehead *et al.* (25) and Fouilland *et al.* (23) was designed to test the effect of different mixing rates within the mixed layer. The two mixing rates tested favored the development of different plankton communities achieving different biomass. Although the UV increases had little impact on bacterial abundance, phytoplankton biomass and community nutrient uptake, the community established under the slower mixing rate was slightly less UV-resistant (23,25). The complexity of food web interactions prevailing in mesocosm experiments makes the testing of the reciprocity of UV effects difficult but the experiment described in Whitehead *et al.* (25) and Fouilland *et al.* (23) suggested that the rate of mixing within the upper mixed layer had no large impact on the measured variables. Clearly, more work is needed on the influence of mixing on UV impacts for communities with kinetics of damage and repair adapted to the prevalent UV regime.

Table 2. Phytoplankton biomass measured during mesocosm experiments.*

Exp no.	Phase of growth	Initial Chl *a* ($\mu g\ L^{-1}$)	Peak Chl *a* ($\mu g\ L^{-1}$)	Final Chl *a* ($\mu g\ L^{-1}$)	Effect of increased UV on phytoplankton biomass
1	Sta, Bloom, Dec	not determined	not determined	not determined	yes, but during bloom only
2	Sta, Bloom	3.5	10	10	yes, but only on week 2 of 4
3	Bloom, Sta, Dec	5	20	5–14	no
4	Sta	1.0	1.5	1.5	no
5	Dec, Sta	1.0	1.0	0.6	no
7	Bloom, Sta	0.8	4–6	4–6	no
8	Bloom, Sta, Dec	1	25	15	yes, but only on day 9 of 10
9	Sta, Dec	5	5	0.5	no
10	Bloom, Dec, Sta	3	9–12	8	no

*The experiment number (Exp no.) refers to that given in Table 1. The three phases of growth identified are stationary (Sta), near-exponential growth (Bloom) and decrease (Dec). Approximate Chl *a* concentrations are taken from published figures. In Exp 1 biomass was estimated from cell counts and *in vivo* fluorescence. No phytoplankton biomass was reported for Exp 6.

The common practice of performing bottle or bag incubations at fixed depths in the mesocosms is producing results that are difficult to interpret in a broad context because of depth and horizontal variations in UV irradiance. Incubations performed close to the surface often show significant inhibition or damage despite the lack of effect on the mesocosms community as a whole (14,15,26). At the very least, fixed-depth incubations exemplify the importance of vertical mixing for the attenuation of UV impacts. However, without a rigorous determination of the UV and PAR irradiances in the whole mesocosm and in the small incubation bag, it cannot be determined unequivocally whether the observed effects are a simple function of the cumulative exposure (which is always much higher in near-surface incubations) or whether physiological mechanisms (*e.g.* reparation of the UV damage at depth in the mesocosms) are also involved. One elegant way to ensure uniform UV exposure on the horizontal plane is to fix the incubation containers on rotating mixing paddles (11).

UV IMPACT ON AUTOTROPHS

Because phytoplankton biomass tends to increase when a water mass is enclosed within a mesocosm, most of the mesocosm experiments reproduced phytoplankton bloom conditions, with Chl *a* biomass increasing up to 25-fold (Table 2). If no nutrient is added to the mesocosms the bloom lasts only for a few days and is quickly followed by a phase of decreasing biomass. It is surprising that statistically significant UV effects on Chl *a* have been observed in only 3 of the 10 experiments reviewed and that these significant effects lasted only a few days (Table 2). Although the number of experiments is too small to identify trends, this lack of effect appears to be independent of the species composition, community structure or geographical location.

Similar to what is observed in laboratory experiments, stationary incubation of water samples close to the water surface in mesocosms often shows inhibitory effect of enhanced UV on phytoplankton photosynthesis (27) and nutrient uptake (26). However, when physiological values are determined for the whole mesocosm population (*e.g.* photosynthesis-irradiance curves, variable fluorescence and photosynthate allocation), these effects are often negligible (14,28). Some of the largest impacts on phytoplankton observed during mesocosm experiments actually have been attributed to direct UV effects on their grazers (27, and below).

Table 3. UV Impact on bacterial abundance and production measured during mesocosm experiments. The experiment number (Exp#) refers to that given in Table 1.

Exp no.	Effect of increased UV on bacterial count	Effect of increased UV on bacterial production
3	Increase	decrease
4	no effect	increase
6	not determined	increase
7	no effect	not determined

UV IMPACT ON BACTERIA

Unlike phytoplankton, bacteria do not rely directly on light for growth, with the notable exceptions of proteorhodopsin-containing bacteria (29) and aerobic photoheterotrophic bacteria (30), so that UV impacts are less coupled to effect of co-occurring PAR irradiance. However, interpretation of mesocosm experiments is complicated by the fact that DOM (their energy source) is strongly affected by UV through phototransformations and photobleaching; nutrient availability for phytoplankton is affected by photochemistry to a much lesser extent. Direct effects on bacteria are difficult to discriminate from indirect impacts on DOM availability (bottom-up control) and impacts on their grazers (top-down control). Only four of the reviewed articles included estimates of bacterial numbers and/or bacterial production (Table 3). UV effects varied from significant increases to significant decreases, likely reflecting different combinations of effects on substrate availability, direct effects on bacteria metabolism and effects on grazers. None of the mesocosm experiments included virus studies, although significant effects of UV on virus abundance and infectivity exist (31).

UV IMPACT ON HETEROTROPHIC PROTISTS AND ZOOPLANKTON

Because the water used to fill mesocosms is generally prefiltered onto 200–1000 μm filter in order to remove large grazers, microzooplankton are the most important consumers in mesocosm studies. Two studies investigated the microzooplankton response to UV increase during mesocosm experiments and they had conflicting results. Although Keller *et al.* (12) found no effect of UV on microzooplankton abundance, Mostajir *et al.* (32) found

a strong negative impact of increased UV on ciliate abundance (66% decrease) and a positive impact on heterotrophic flagellates (up to a 400% increase) but no significant effect of UV increases on microzooplankton bacterivory was detected (33).

The relatively large volume (13 000 L) of the mesocosms used by Keller *et al.* (11,12) allowed the inclusion of zooplankton populations. In well-mixed mesocosms they found a tendency (sometimes significant) for zooplankton abundance to be lower under UV-enhanced treatment, compared with controls, and explained this by a combination of direct and indirect effects (11). Similar results were obtained in stratified mesocosms (12), although increased mortality of copepod nauplii in UV-enhanced treatment did not translate into lower abundance of copepodite or adult copepods.

UV IMPACT ON PLANKTONIC FOOD WEB AND COMMUNITY STRUCTURE

On the basis of the above discussion of the compartments of the marine microbial food web, it is obvious that a large discrepancy exists between the UV sensitivity of the different biological components and that this sensitivity is a function of nutrient status, preacclimation, mixing regime and community composition. Species respond differently to environmental changes and the various behavioral and physiological processes among members of one species (*e.g.* reproduction, cell division, photosynthesis and respiration) are also affected differently by any one environmental change (34). Moreover, the response of a species to change in UV irradiance is modulated by how other species in the community respond to this environmental change (35). As a result of the differential susceptibility to UV, it is therefore not surprising that a common conclusion of many mesocosm studies (but not all; see the article by Sommaruga (35)) is that changes in community composition affect the structure and functioning of the system exposed to enhanced UV.

Changes in planktonic community structure (species composition and size distribution) are important because they may translate into significant alteration of carbon and nutrient cycling in the marine system (36). Mostajir *et al.* (32) were able to establish a carbon biomass budget for mesocosms exposed to natural levels and enhanced levels of UV during a week-long experiment. They found no impact on the overall biomass accumulation but a large impact of UV enhancement on the carbon biomass partitioning among the 5 different compartments examined (ciliates, heterotrophic flagellates, heterotrophic bacteria, autotrophic flagellates and diatoms) (Table 4). In that experiment the biomass of the larger organisms (ciliates and diatoms) was lower under UV-enhanced treatments, whereas the biomass of the smaller organisms was higher. Mostajir *et al.* (32) concluded that UV enhancement could induce a shift in the planktonic community structure towards smaller organisms more typical of the microbial loop, with implications on carbon transfer.

In ecosystem-level experiments, it is difficult to discriminate between direct UV effects and effects propagated through the food web (*e.g.* impact on the prey or grazer/predator of the organisms of interest). One promising approach to this problem is the study of ecological interactions through the analysis of multispecies time-series data using first-order multivariate autoregressive models (37). The simultaneous study of every compartment of the planktonic food web requires a lot of work from multiple investigators but the insights gained from such integrative studies are of great value and misleading conclusions are much less likely to occur.

Table 4. Carbon biomass of ciliates, heterotrophic flagellates, heterotrophic bacteria, autotrophic flagellates and diatoms at T_0 and at the end of the experiment on day 7 and difference between the two treatments.*

Planktonic compartment	T_0 ($\mu g\ C\ L^{-1}$)	Day 7 Natural UV-B ($\mu g\ C\ L^{-1}$)	Day 7 Enhanced UV-B ($\mu g\ C\ L^{-1}$)	Difference between the 2 treatments (%)
Ciliates	1	11	4	−64
Heterotrophic flagellates	11	35	79	126
Bacteria	19	31	46	48
Autotrophic flagellates	50	420	1100	162
Diatoms	203	1330	590	−56
Sum of the 5 compartments	284	1827	1819	−0.4

*Biomasses were measured in duplicate mesocosms exposed to natural or enhanced UV-B. Data are adapted from Mostajir *et al.* (32).

FUTURE RESEARCH

Many aspects of the UV photobiology and photochemistry of planktonic marine ecosystems deserve further attention. Notably, no mesocosm experiment so far has addressed the UV effects on oligotrophic offshore communities where small phytoplankton cells (such as the cyanobacteria *Synechococcus*) and a microbial food web dominate. Only two studies so far have included zooplankton grazers, although they represent an essential link of the food web and they are sensitive to UV at different stages in their life (38). Longer-term studies would also provide essential information on the recovery and protection from UV stress and the adaptation to this stress that can be exhibited by marine plankton. However, artifacts are more likely when organisms are kept in mesocosms for a long period.

One important aspect of UV research that has been neglected so far in mesocosm experiments is the partitioning of photon absorption within the mesocosms. Optical properties are important because the main determinants of average exposure in the mixed layer are the transparency of the water column and the depth of that mixed layer. While photobleaching occurs in the confined water column of a mesocosm and plankton biomass changes over time, the relative contribution of water molecules, CDOM, phytoplankton and nonalgal particle also changes. It is possible that some of the effects attributed to changes in nutrient concentration in the mesocosms or to UV acclimation of the organisms were in fact related to changes in the absorption coefficient partitioning.

The synergy between UV and other stressors have been the subject of many studies, including some experiments using mesocosms (23,26). Global temperature increase, coastal eutrophication, petroleum and toxic spills and other current and forecasted changes will interact with UV photochemistry and photobiology (34,39–41). Mesocosm experiments would complement our understanding of the complex interactions between these stresses in a way that simple laboratory experiments may not reveal.

Extrapolation of results from enclosed experimental ecosystems to the natural environment represents a significant challenge (7,42). The scales selected for a mesocosm study should reflect the delicate balance between control, realism and generality (6,7). The scaling theory and the results from experiments directly addressing the effect of scale on ecological processes are offering tools on how we can extrapolate from small-scale, short-term experiments involving simplified ecosystems to complex, natural systems (42). One way

of validating the findings of mesocosm experiments is to establish comparisons with data collected from a range of natural ecosystems. Although the number of confounding variables in the field is large, the most significant effects observed in mesocosms are likely to show up in well-focused comparisons with data from natural ecosystems.

CONCLUSION

Ideally, experiments reveal interactions, expose underlying mechanisms and support or refute models (43). Mesocosm experiments have shown that, despite UV enhancements that were often far greater than could result from ozone depletion, planktonic communities do not suffer from the catastrophic negative impacts that might have been inferred from some laboratory experiments on individual component of the marine food web. In their modeling of water column photosynthesis Neale *et al*. (44) agreed with this view, calculating that a 50% ozone depletion would cause at most a 1.5–8% reduction of water column phytoplankton production in the Weddell-Scotia Confluence of the Southern Ocean, depending on the mixing scenario. By comparison, realistic changes in cloudiness alone could induce changes of −24% to +6%. Similarly, on the basis of their numerical model incorporating vertical mixing and satellite-derived distributions of stratospheric ozone, sea ice, clouds, surface temperature and phytoplankton biomass, Arrigo *et al*. (45) estimated that the loss of primary production in the Southern Ocean resulting from enhanced fluxes of UV-B due to severe ozone depletion was <0.25%.

Some of the UV enhancement used in the reviewed experiments may seem unrealistic in view of likely changes in UV irradiance due to ozone depletion. However, factors such as changes in stratification, snow and ice cover or modification of UV-absorbing terrestrial DOM input to the sea may cause changes in UV exposure much greater than would result from severe ozone depletion (46,47). Therefore, even the largest UV enhancement may well be representative of future modifications linked to global changes. As previously noted, the relatively small effects of UV enhancement observed in mesocosm experiments must be put in perspective by recognition that the ''normal'' levels of UV already have significant effects (44,45). This is supported by significant differences observed between the natural and UV-B–excluded treatments of mesocosm experiments (32,33).

Mesocosm experiments can have a quantitative predictive goal or reveal general mechanisms likely to apply to a wide variety of systems (43). Mesocosm studies of the UV impact on marine plankton sometimes have a poor predictive value because of scale issues, because not all trophic levels are represented or because not every key environmental condition is reproduced in mesocosms. Nevertheless, valuable insights into the controls and mechanisms of UV damage and repair have been gained and these experiments begin to reveal the complex interactions between UV and other stressors (*e.g*. grazing and nutrient depletion). Together with laboratory experiments, observations from the marine ecosystem and models, insights gained from mesocosm experiments will continue to improve our understanding of the marine plankton and help to predict the impacts of current and forecasted environmental changes.

Acknowledgements—We thank the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Inter American Institute for Global Change Research (IAI; grant CRN-26) for funding support. Comments from two anonymous reviewers improved the manuscript.

REFERENCES

1. de Mora, S. J., S. Demers and M. Vernet (2000) *The Effects of UV Radiation in the Marine Environment*. Cambridge University Press, Cambridge.
2. Hessen, D. O. (2002) *UV Radiation and Arctic Ecosystems*. Springer, Berlin.
3. Helbling, E. W and H. E. Zagarese (2003) *UV Affects in Aquatic Organisms and Ecosystems*. Comprehensive Series in Photochemistry and Photobiology, Vol. 1. The Royal Society of Chemistry and Springer Verlag, Cambridge.
4. Vincent, W. F. and P. J. Neale (2000) Mechanisms of UV damage to aquatic organisms. In *The Effects of UV Radiation in the Marine Environment* (Edited by S. J. de Mora, S. Demers and M. Vernet), pp. 149–176. Cambridge University Press, Cambridge.
5. Roy, S. (2000) Strategies for the minimisation of UV-induced damage. In *The Effects of UV Radiation in the Marine Environment* (Edited by S. J. de Mora, S. Demers and M. Vernet), pp. 177–205. Cambridge University Press, Cambridge.
6. Kemp, W. M., J. E. Petersen and R. H. Gardner (2001) Scale-dependence and the problem of extrapolation: Implications for experimental and natural coastal ecosystems. In *Scaling relations in experimental ecology* (Edited by R. H. Gardner, W. M. Kemp, V. S. Kennedy and J. E. Petersen), pp. 3–57. Columbia University Press, New York.
7. Petersen, J. E., W. M. Kemp, R. Bartleson, W. R. Boynton, C.-C. Chen, J. C. Cornwell, R. H. Gardner, D. C. Hinkle, E. D. Houde, T. C. Malone, W. P. Mowitt, L. Murray, L. P. Sanford, J. C. Stevenson, K. L. Sundberg and S. E. Suttles (2003) Multiscale experiments in coastal ecology: Improving realism and advancing theory. *BioScience* **53**, 1181–1197.
8. Carpenter, S. R. (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* **77**, 677–680.
9. Grice, G. D. and M. R. Reeve (1982) *Marine mesocosms: Biological and chemical research in experimental ecosystems*. Springer-Verlag, New York.
10. Huston, M. A. (1999) Microcosm experiments have limited relevance for community and ecosystem ecology: Synthesis of comments. *Ecology* **80**, 1088–1089.
11. Keller, A., P. Hargraves, H. Jeon, G. Klein-MacPhee, E. Klos, C. Oviatt and J. Zhang (1997) Ultraviolet-B radiation enhancement does not affect marine trophic levels during a winter-spring bloom. *Écoscience* **4**, 129–139.
12. Keller, A., P. Hargraves, H. Jeon, G. Klein-MacPhee, E. Klos, C. Oviatt and J. Zhang (1997) Effect of ultraviolet-B enhancement on marine trophic levels in a stratified coastal system. *Mar. Biol.* **130**, 277–287.
13. Wängberg, S.-Å., A. Wulff, C. Nilsson and U. Stagell (2001) Impacts of UV-B radiation on microalgae and bacteria: A mesocosm study with computer modulated UV-B radiation addition. *Aquat. Microb. Ecol.* **25**, 75–86.
14. Bouchard, J. N., D. A. Campbell and S. Roy (2005) Effects of UV-B radiation on the D1 protein repair cycle of natural phytoplankton communities from three latitudes (Canada, Brazil and Argentina). *J. Phycol.* **41**, 273–286.
15. Longhi, M. L., G. A. Ferreyra, I. Schloss and S. Roy (2006) Variable phytoplankton response to enhanced UV-B and nitrate addition in mesocosm experiments at three latitudes (Canada, Brazil and Argentina). *Mar. Ecol. Prog. Ser.* **313**, 57–72.
16. Steeneken, S. F., A. G. J. Buma and W. W. C. Gieskes. (1995) Changes in transmission characteristics of polymethylmethacrylate and cellulose(III) acetate during exposure to ultraviolet light. *Photochem. Photobiol.* **61**, 276–280.
17. Kirk, J. T. O. (1994) Optics of UV-B radiation in natural waters. *Arch. Hydrobiol. Beih.* **43**, 1–16.
18. Belzile, C., W. F. Vincent, C. Howard-Williams, I. Hawes, M. R. James, M. Kumagai and C. S. Roesler (2004) Relationships between spectral optical properties and optically active substances in a clear oligotrophic lake. *Water Resour. Res.* **40**, W12512 (DOI: 10.1029/2004WR003090).
19. Belzile, C., S. Demers, D. R. S. Lean, B. Mostajir, S. Roy, S. de Mora, D. Bird, M. Gosselin, J.-P. Chanut and M. Levasseur (1998) An experimental tool to study the effects of ultraviolet radiation on

planktonic communities: A mesocosm approach. *Environ. Technol.* **19**, 667–682.
20. Riley, G. A. (1957) Phytoplankton of the North Central Sargasso Sea. *Limnol. Oceanogr.* **2**, 252–270.
21. Neale, P. J. (2000) Spectral weighting functions for quantifying effects of UV radiation in marine ecosystems. In *The Effects of UV Radiation in the Marine Environment* (Edited by S. J. de Mora, S. Demers and M. Vernet), pp. 72–100. Cambridge University Press, Cambridge.
22. Neale, P. J., E. W. Helbling and H. E. Zagarese (2003) Modulation of UVR exposure and effects by vertical mixing and advection. In *UV Effects in Aquatic Organisms and Ecosystems* (Edited by E. W Helbling and H. E. Zagarese), pp. 107–134. Comprehensive Series in Photochemistry and Photobiology, Vol. 1. The Royal Society of Chemistry and Springer Verlag, Cambridge.
23. Fouilland, E., M. Gosselin, B. Mostajir, M. Levasseur, J.-P. Chanut, S. Demers and S. de Mora (2003) Effects of ultraviolet-B radiation and vertical mixing on nitrogen uptake by a natural planktonic community shifting from nitrate to silicic acid deficiency. *Limnol. Oceanogr.* **48**, 18–30.
24. Cullen, J. J. and M. P. Lesser (1991) Inhibition of photosynthesis by ultraviolet radiation as a function of dose and dosage rate: Results for a marine diatom. *Mar. Biol.* **111**, 183–190.
25. Whitehead, R. F., S. de Mora, S. Demers, M. Gosselin, P. Montfort and B. Mostajir (2000) Interactions of ultraviolet-B radiation, mixing, and biological activity on photobleaching of natural chromophoric dissolved organic matter: A mesocosm study. *Limnol. Oceanogr.* **45**, 278–291.
26. Fauchot, J., M. Gosselin, M. Levasseur, B. Mostajir, C. Belzile, S. Demers, S. Roy and P. Z. Villegas (2000) Influence of UV-B radiation on nitrogen utilization by a natural assemblage of phytoplankton. *J. Phycol.* **36**, 484–496.
27. Mostajir, B., T. Sime-Ngando, S. Demers, C. Belzile, S. Roy, M. Gosselin, J.-P. Chanut, S. de Mora, J. Fauchot, F. Vidussi and M. Levasseur (1999) Ecological implications of changes in cell size and photosynthetic capacity of marine Prymnesiophyceae induced by ultraviolet-B radiation. *Mar. Ecol. Prog. Ser.* **187**, 89–100.
28. Wängberg, S.-Å., K. Garde, K. Gustavson and J.-S. Selmer (1999) Effects of UVB radiation on marine phytoplankton communities. *J. Plankton Res.* **21**, 147–166.
29. Béjà, O., E. N. Spudich, J. L. Spudich, M. LeClerc and E. F. DeLong (2001) Proteorhodopsin phototrophy in the ocean. *Nature* **411**, 786–789.
30. Kolber, Z. S., F. G. Plumley, A. S. Lang, J. T. Beatty, R. E. Blankenship, C. L. VanDover, C. Vetriani, M. Koblizek, C. Rathgeber and P. G. Falkowski (2001) Contribution of aerobic photoheterotrophic bacteria to the carbon cycle in the ocean. *Science* **292**, 2492–2495.
31. Jeffrey, W. H., J. P. Kase and S. W. Wilhelm (2000) UV radiation effects on heterotrophic bacterioplankton and viruses in marine ecosystems. In *The Effects of UV Radiation in the Marine Environment* (Edited by S. J. de Mora, S. Demers and M. Vernet), pp. 206–236. Cambridge University Press, Cambridge.
32. Mostajir, B., S. Demers, S. de Mora, C. Belzile, J.-P. Chanut, M. Gosselin, S. Roy, P. Z. Villegas, J. Fauchot, J. Bouchard, D. Bird, P. Monfort and M. Levasseur (1999) Experimental test of the effect of ultraviolet-B radiation in a planktonic community. *Limnol. Oceanogr.* **44**, 586–596.
33. Chatila, K., S. Demers, B. Mostajir, M. Gosselin, J.-P. Chanut and P. Montfort (1999) Bacterivory of a natural heterotrophic protozoan community exposed to different intensities of ultraviolet-B radiation. *Aquat. Microb. Ecol.* **20**, 59–74.
34. Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, J. Elster, I. S. Jónsdóttir, K. Laine, K. Taulavuori, E. Taulavuori and C. Zöckler (2004) Responses to projected changes in climate and UV-B at the species level. *Ambio* **33**, 418–435.
35. Sommaruga, R. (2003) UVR and its effects on species interactions. In *UV Effects in Aquatic Organisms and Ecosystems* (Edited by E. W Helbling and H. E. Zagarese), pp. 485–508. Comprehensive Series in Photochemistry and Photobiology, Vol. 1. The Royal Society of Chemistry and Springer Verlag, Cambridge.
36. Legendre, L. and F. Rassoulzadegan (1995) Plankton and nutrient dynamics in marine waters. *Ophelia* **41**, 153–172.
37. Ives, A. R., B. Dennis, K. L. Cottingham and S. R. Carpenter (2003) Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.* **73**, 301–330.
38. Zagarese, H. E. and C. E. Williamson. 2000. Impact of solar UV radiation on zooplankton and fish. In: *The Effects of UV Radiation in the Marine Environment* (Edited by S. J. de Mora, S. Demers and M. Vernet), pp. 277–309. Cambridge University Press, Cambridge.
39. Zepp, R. G., T. V. Callaghan and D. J. Erickson III (2003) Interactive effects of ozone depletion and climate change on biogeochemical cycles. *Photochem. Photobiol. Sci.* **2**, 51–61.
40. Sargian, P., B. Mostajir, K. Chatila, G. A. Ferreyra, E. Pelletier and S. Demers (2005) Non-synergistic effects of water-soluble crude oil and enhanced ultraviolet-B radiation on a natural plankton assemblage. *Mar. Ecol. Prog. Ser.* **294**, 63–77.
41. Sargian, P., E. Pelletier, B. Mostajir, G. A. Ferreyra and S. Demers (2005) TBT toxicity on a natural planktonic assemblage exposed to enhanced ultraviolet-B radiation. *Aquat. Toxicol.* **73**, 299–314.
42. Gardner, R. H., W. M. Kemp, V. S. Kennedy and J. E. Petersen (2001) *Scaling Relations in Experimental Ecology.* Columbia University Press, New York.
43. Pace, M. L. (2001) Getting it right and wrong: Extrapolations across experimental scale. In *Scaling Relations in Experimental Ecology* (Edited by R. H. Gardner, W. M. Kemp, V. S. Kennedy and J. E. Petersen), pp. 157–177. Columbia University Press, New York.
44. Neale, P. J., R. F. Davis and J. J. Cullen (1998) Interactive effects of ozone depletion and vertical mixing on photosynthesis of Antarctic phytoplankton. *Nature* **392**, 585–589.
45. Arrigo, K. R., D. Lubin, G. L. van Dijken, O. Holm-Hansen and E. Morrow (2003) Impact of a deep ozone hole on Southern Ocean primary production. *J. Geophys. Res.* **108**, 3154 (DOI:10.1029/2001JC001226).
46. Pienitz, R. and W. F. Vincent (2000) Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. *Nature* **404**, 484–487.
47. Vincent, W. F. and C. Belzile (2002) UV effects on aquatic microbial food webs in northern lakes and rivers. In: *UV Radiation and Arctic Ecosystems* (Edited by D. O. Hessen), pp. 137–155. Springer, Berlin.
48. Chatila, K., S. Demers, B. Mostajir, M. Gosselin, J.-P. Chanut, P. Montfort and D. Bird (2001) The response of natural bacterioplankton community to different levels of ultraviolet-B radiation: A food web perspective. *Microb. Ecol.* **41**, 56–68.
49. Mousseau L, M. Gosselin, M. Levasseur, S. Demers, J. Fauchot, S. Roy, P. Z. Villegas and B. Mostajir (2000) Long-term effects of ultraviolet-B radiation on community structure and on simultaneous uptake of carbon and nitrogen by estuarine phytoplankton during a mesocosm study. *Mar. Ecol. Prog. Ser.* **199**, 69–81.
50. Gustavson, K., K. Garde, S.-Å. Wängberg and J.-S. Selmer (2000) Influence of UV-B radiation on bacterial activity in coastal waters. *J. Plankton Res.* **22**, 1501–1511.