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REVIEW AND SYNTHESIS

Effects of UVB radiation on marine and freshwater organisms: a synthesis through meta-analysis

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Abstract

Ultraviolet-B (UVB) radiation is a global stressor with potentially far-reaching ecological impacts. In the first quantitative analysis of the effects of UVB on aquatic organisms, we used meta-analytic techniques to explore the effects of UVB on survival and growth in freshwater and marine systems. Based on the large body of literature on the effects of UVB in aquatic systems, we predicted that UVB would have different effects in different habitats, experimental venues, trophic groups and life history stages. Contrary to our predictions, we found an overall negative effect of UVB on both survival and growth that crossed life histories, trophic groups, habitats and experimental venues. UVB had larger negative effects on growth in embryos compared with later life history stages. Despite the overall negative effect of UVB, effect sizes varied widely. In the survival analyses, no relationship between mean effect size and taxonomic groups or levels of exposure to UVB was detected. In the growth analyses, a larger negative effect on protozoans was observed. Our analyses suggest that the effects of UVB in aquatic systems are large and negative but highly variable between organisms. Variation in susceptibility may have important implications for population and community structure.

Keywords

Aquatic systems, consumer, environmental stress, global change, growth, life history, meta-analysis, primary producer, survival, ultraviolet-B.

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INTRODUCTION

Stratospheric ozone depletion and the concomitant increase in ultraviolet-B (UVB) radiation pose an important threat to ecological systems. The work of Molina & Rowland (1974) on ozone-degrading compounds and the discovery of the Antarctic ozone hole (Farman *et al.* 1985) were influential in the formulation and signing of the Montreal Protocol on Substances that Deplete the Ozone Layer in 1987. This landmark international treaty was designed to halt the production and use of CFCs to avoid further degradation of the ozone layer. Despite the success of the Montreal Protocol (Blaustein *et al.* 2003; Solomon 2004), the ozone layer remains damaged. This damage results in increasing levels of UVB radiation reaching the earth's surface (Kerr & McElroy 1993; Madronich 1993, 1994; Madronich *et al.* 1998; Solomon 1999).

Ultraviolet-B radiation negatively impacts organisms in both terrestrial and aquatic systems (Caldwell *et al.* 1998; Häder *et al.* 1998). Within living cells, nucleic acids, proteins and lipids are the primary targets of UVB damage (Buma *et al.* 2003). Cyclobutane pyrimidine dimers (CPDs) in DNA are the most common lesion induced by UVB exposure. These dimers as well as other types of UV-induced DNA damage can inhibit transcription and replication (Buma *et al.* 2003). Damage to proteins can interfere with normal cellular processes, while damage to lipids can disrupt cell membranes. Many organisms are able to repair damage caused by UVB radiation. Of these repair mechanisms, DNA repair is the most studied process. Organisms use different types of DNA repair mechanisms including photorepair, excision repair and post-replication repair (Tevini 1993). Photorepair is mediated by a group of enzymes called photolyases and relies on radiant energy in the UVA and photosynthetically active radiation (PAR) bands (Kelner 1949; Sancar & Sancar 1988). Photolyases primarily remove CPDs. Excision repair and post-replication repair are independent of radiant energy but are less efficient at repairing CPDs. Repair efficiencies can differ between species (e.g. Blaustein *et al.* 1994). Many experiments on the effects of UVB have been

conducted in the laboratory (e.g. Damkaer *et al.* 1981; Charron *et al.* 2000; Roleda *et al.* 2004a). Although these experiments use ambient levels of UVB, researchers rarely replicate the full spectral environment found in natural systems. Because photorepair relies on wavelengths spanning UVA and PAR, laboratory experiments that do not carefully modulate the ratio of UVB to UVA and PAR may overemphasize the effects of UVB (Day & Neale 2002).

At the organismal level, damage to DNA, proteins and lipids may result in a variety of lethal and sublethal effects. These effects have been reported in many organisms including viruses and bacteria (Karentz *et al.* 1994), phytoplankton and algae (Häder *et al.* 2003), amphibians and fish (Blaustein *et al.* 1998; Hessen 2003), crops and forests (Caldwell *et al.* 1998), crustaceans (Hessen 2003) and humans (van der Leun & de Gruijl 1993). The effects of UVB radiation on organisms in aquatic habitats are of particular concern (Häder 1993).

The effects of UVB on aquatic organisms depend in part on the dose of harmful radiation to which an individual organism is exposed. UVB dose is affected by both organismal behaviour/location within the water column and the optical characteristics (i.e. UVB transmittance) of the water body. UVB penetration in aquatic habitats is modulated by factors including dissolved organic carbon (DOC), suspended particles (including phytoplankton) and surface reflection (Díaz *et al.* 2000; Hargreaves 2003). In most aquatic habitats, UV attenuation is controlled primarily by absorption of UVB energy by DOC (Scully & Lean 1994). As the majority of DOC is derived from terrestrial sources, freshwater habitats generally show higher UVB attenuation (and therefore lower levels of UVB in the water column) compared to marine waters (Kirk 1994). Thus, marine organisms and freshwater organisms inhabiting clear alpine lakes may be most at risk to damage caused by recently increased UVB radiation.

In some communities, organisms at lower levels in a food web tend to be more susceptible to environmental stress (Rafaelli 2004). Aquatic autotrophs, including those inhabiting the shallow benthos, are generally exposed to some level of UVB. Several studies have shown negative effects of UVB on photosynthetic rates in aquatic systems (Han *et al.* 2003; Roleda *et al.* 2004a; Litchman & Neale 2005). Unlike benthic autotrophs, phytoplankton are found throughout the water column and can be exposed to high levels of UVB (Villafañe *et al.* 2003). In addition, phytoplankton tend to be small in size and therefore have short pathlengths, allowing UVB penetration deep into the cells (Day & Neale 2002). These observations have led to the speculation that phytoplankton may be particularly susceptible to damage from UVB radiation (Häder 1993; Day & Neale 2002; but see Halac *et al.* 1997). While photosynthetic organisms must inhabit the photoactive zone, consumers (particularly mobile consumers) may behaviourally avoid regions of high UVB within the water column by using refugia or seeking deeper waters (reviewed in Leech & Johnsen 2003). However, other constraints such as foraging behaviour, avoiding predation or thermal requirements could force consumers into areas with high UVB exposure (Leech & Johnsen 2003). Consumers at these higher trophic levels in aquatic systems experience direct negative effects from UVB radiation (Siebeck *et al.* 1994; Williamson 1995; Blaustein *et al.* 1998; Hessen 2003). UVB causes mortality in some species of zooplankton, amphibians and fish (Siebeck *et al.* 1994; Blaustein & Belden 2003; Hessen 2003). Sublethal effects such as reduced growth, behavioural changes and increased susceptibility to disease have also been reported (e.g. Williamson *et al.* 1997; Belden *et al.* 2000; Salo *et al.* 2000).

The effects of UVB can vary over life history stage in both consumers and primary producers. Some life history stages may be less adept at repair or have habitat requirements that place the organism in areas with high UVB exposure (e.g. Siebeck *et al.* 1994; Epel *et al.* 1999; McNamara & Hill 1999). For example, brine shrimp (*Artemia franciscana*) are more susceptible to damage from UVB in naupliar stages compared to the adult stage (Dattilio *et al.* 2005). Early life history stages of autotrophic organisms can also be more susceptible to damage from UVB. For example, early life history stages of some macroalgae are more susceptible to damage than the later stages (e.g. Roleda *et al.* 2004b). Embryos may be particularly susceptible to damage from UVB due to reduced capacity for repair and limited mobility (Epel *et al.* 1999).

Lethal and sublethal effects of UVB on both primary producers and consumers can cause shifts in community structure and function and thus can impact overall ecological processes in both aquatic and terrestrial systems (see reviews in de Mora *et al.* 2000; Hessen 2003). For example, one half of all photosynthetic production is due to the activities of phytoplankton in aquatic systems (Houghton & Woodwell 1989; Zepp 2003). UVB radiation may alter community composition, size distribution, productivity, or nutritional quality of algae and photosynthetic bacteria (Karentz *et al.* 1994). Reductions in the biomass and photosynthetic yield of phytoplankton may reduce the available carbon sink in the oceans, resulting in higher atmospheric CO_2 concentrations (Zepp 2003). Shifts in phytoplankton community composition, size distribution and nutritional quality could reduce the resources available to higher trophic levels.

The potential of UVB to act as a stressor in aquatic environments has led to a number of reviews of the effects of UVB in both freshwater and marine systems (e.g. Häder 1993; Karentz *et al.* 1994; Siebeck *et al.* 1994; Häder *et al.* 1998, 2003; de Mora *et al.* 2000; Helbling & Zagarese 2003).

However, organisms vary widely in their responses to UVB: some species are highly susceptible while others appear to be relatively resilient. Moreover, even within a species, susceptibility may differ between populations and in different life history stages. Many reviews focus on the observed variation in susceptibility between organisms. A synthetic analysis of the overall effects of UVB is lacking.

Previous reviews on the effects of UVB in aquatic systems have been qualitative. In general, these reviews present lists of effects and use the reported statistical significance of each study to assess the magnitude of the effects of UVB radiation. However, assessing the strength of an effect or importance of a stressor by counting the proportion of studies reporting a significant result (i.e. 'vote-counting') has poor statistical power (Rosenberg *et al.* 2000). Meta-analysis techniques avoid the problems of conventional vote-counts and the subjectivity of traditional reviews. Meta-analyses have been used to identify broad trends in several aspects of global change (e.g. Root *et al.* 2003).

We used meta-analytic techniques to test several hypotheses regarding the effects of UVB radiation in aquatic systems. For each hypothesis, we tested the effects of UVB on survival and growth separately. We hypothesized that UVB radiation has a negative effect on survival and growth of aquatic organisms. Furthermore, we hypothesized that the effect of UVB would be larger (1) in marine systems compared to freshwater habitats, (2) in the laboratory compared to field studies, (3) in primary producers compared to consumers, and (4) in earlier life history stages compared to later stages. Our paper is the first quantitative review of the effects of UVB in aquatic systems using rigorous statistical procedures. Our analyses reveal a large negative effect of UVB radiation on both survival and growth across all habitats, experimental venues, trophic groups and life history stages.

MATERIALS AND METHODS

Data selection

We used six electronic databases (BIOSIS, Web of Science, Aquatic Sciences & Fisheries Abstracts, Fish & Fisheries Worldwide, Wildlife & Ecology Studies Worldwide, and Biological & Agricultural Index) to identify the studies used in our analyses. Within these databases, we searched for all combinations of the terms: *ultraviolet*, *UV*, *UVB* with *survival*, *growth*, and *mortality* to find primary literature on the effects of UVB radiation in aquatic organisms. We limited our search to experimental manipulations of UVB radiation (i.e. not UVA or UVA combined with UVB) where the investigators used the standard technique of applying plastic filters that differentially transmitted or filtered out UVB radiation. To explore both the lethal and sublethal effects of UVB, we selected mortality and growth as response variables. Other sublethal response variables are possible (i.e. reproduction and life stage duration) but growth is commonly measured for many organisms and can be assessed for multiple life stages. To avoid potential biases in the selection of studies, we established criteria for the inclusion of a study in the meta-analyses *a priori* (see Appendix S1 in Supplementary Material). Any data points within an article that met the criteria were considered for inclusion. To avoid personal bias, we made no attempt to judge study quality.

Several articles included more than one species, location (e.g. lakes with different spectral transmission properties), UVB irradiance (or dose) or sampling period. All species and locations from a given article were included in our analyses if the overall criteria for including the study were met. Although including all species or locations from one study might decrease the independence among some data points, the inclusion of all available species and environments allowed us to more fully explore the effects of UVB radiation in these systems (Gurevitch *et al.* 1992; Searles *et al.* 2001). However, if more than one ambient UVB irradiance or dose were used in the original article we randomly selected only one irradiance level or dose for inclusion. If the article reported survival or growth over a time series, we selected the final measurement for these analyses. When articles quantified growth using several response variables (i.e. length and mass), we randomly selected one variable for inclusion.

All data were obtained from primary research articles. When necessary, data were extracted from published figures using TechDig V.2.0 software, available at http://home.xnet.com/ronjones/#TECHDIG). We used the ITIS Catalogue of Life: 2005 Annual Checklist (http://annual.sp2000.org/2005/search.php) for taxonomic information. We followed the classification given by the authors for life history stage; thus some categories may include photosynthetic organisms and non-photosynthetic organisms (e.g. 'embryo') while other categories may be specific to certain taxa (e.g. 'sporophyte').

Effect sizes

Our primary goal was to calculate an overall measure, including magnitude and direction (positive or negative), of the effect of UVB radiation on survival and growth in aquatic organisms. We used Hedges' *d* as our metric of standardized effect size (Hedges & Olkin 1985). Hedges' *d* is an unbiased weighted measure of the difference between the means of the control and experimental groups divided by the pooled standard deviation and multiplied by a correction term to adjust for small samples sizes. Convention dictates that a value of *d* greater than or equal to 0.8 is a large effect,

d equal to 0.5 is a moderate effect and *d* equal to 0.2 is a small effect (Cohen 1969; Gurevitch *et al.* 1992). We defined the control group as the group shielded from UVB radiation; therefore, a negative value of *d* indicates a negative effect of UVB on survival or growth. We also calculated a log response ratio (lnR) as a measure of effect size, but because the results were qualitatively similar using both measures, we report only those based on *d*. The only differences between the two metrics are a significantly larger effect of UVB on growth in primary producers compared to consumers, a larger (although not significantly larger) effect of UVB on growth in adult stages compared to embryos and larvae, and a nonsignificant effect of UVB on growth in field studies and on the larval life history stage (see Supplementary Figs S1 and S2 for comparison of *d* with lnR). We used MetaWin Version 2.0 (Rosenberg *et al.* 2000) for all statistical procedures.

We identified 115 articles with primary data on the effects of UVB radiation on survival. Of those, only 46 met our criteria, generating 87 total comparisons of 61 species (Table S1). Of the 87 comparisons, a significant difference in survival between UVB exposed and UVB shielded organisms was reported in 39 comparisons. We found 71 studies on the effects of UVB on growth in our searches. Only 27 of these met our criteria. The articles used in the analysis yielded 46 comparisons of 32 different species (Table S2). Out of the 46 comparisons, a significant difference in growth between UVB exposed organisms and UVB shielded organisms was reported in 29 comparisons (Table S2).

Full models

We selected our response variables with the intention of quantifying both lethal and sublethal effects. As such, we used all survival data in one analysis and all growth data in a separate analysis. We used a random effects model to calculate the grand mean effect size for each analysis. Although fixed effects models are more typical in meta-analyses, we expected the true effect size to vary among studies due to the broad taxonomic scope of these analyses: thus, a random effects model was necessary (Gurevitch & Hedges 1999). Random effects models use the pooled standard deviation to estimate the distribution of effect sizes within the population. Therefore, using a random effects model allows effect size estimates to vary not only due to sampling error, but due to real biological or environmental differences between organisms and studies.

The output of each statistical test consisted of the grand mean effect size for the analysis with an accompanying bias-corrected bootstrapped 95% confidence interval (CI) (Adams *et al.* 1997) and a total heterogeneity statistic (Q). The mean effect size is significantly different from zero if the CIs do not overlap with zero. The heterogeneity statistic is a weighted sum of squares and is tested against a chi-square distribution with $n - 1$ degrees of freedom. A significant value of Q in a random effects model indicates that the variation among effect sizes is greater than expected from sampling error and the random component included in the model, suggesting that all effect sizes may not come from the same population (Rosenberg *et al.* 2000).

Exploratory analyses

Our secondary goal was to examine the similarity in effect size among *a priori* selected groups including trophic group, habitat, life history stages or experimental venue. We performed separate exploratory analyses testing the heterogeneity of mean effect sizes between groups using mixed effects models. This method of analysis is not ideal and is problematic in most cases. Performing multiple analyses on the same dataset increased the chance of Type I error. However, the purpose of these analyses was to quantify patterns in the literature, not to explain or partition heterogeneity. This distinction is subtle but important: future analyses should not use these methods to partition variance, but rather use hierarchical analytic methods (below, under Sources of heterogeneity within groups). Due to low sample sizes in some groups, performing multiple analyses was the only way to explore the patterns in the literature. In addition, as groups with fewer than four comparisons were removed from the analyses, two of the four exploratory analyses used a subset of the data (trophic groups and developmental stages). We compared the mean effect size between marine and freshwater organisms, between studies conducted in the laboratory (and therefore under artificial UVB radiation) and studies conducted in the field (here defined as any experiment with natural solar radiation), between trophic groups and between developmental stages. A mean effect size and bias-corrected bootstrapped 95% CI were calculated for each group in the exploratory analyses. We report parametric 95% CIs when group sample size is small (i.e. < 10) because parametric CIs provide a more conservative error estimate. When significant differences in mean effect size between three or more groups were observed in these exploratory analyses, we adjusted α using the Bonferroni method prior to conducting multiple two-way tests to determine where significant differences occurred (Gotelli & Ellison 2004). Heterogeneity statistics were calculated to quantify both within-group (Q_W) and between-group (Q_B) variation. The interpretation of significant values of Q in mixed effects models is similar to random effects models. However, mixed effects models also incorporate group differences. In mixed effects models, significant values of Q suggest that observed variation is greater than expected due to sampling

error, real variation in effect sizes (random component of model) and group differences (Gurevitch & Hedges 1999). Although using only additive models may obscure some relationships (e.g. if embryos in freshwater habitats are more susceptible to damage from UVB compared to embryos in marine habitats our models would not detect the difference), current factorial meta-analytic techniques are only appropriate for use when the original studies are factorial in structure (Gurevitch *et al.* 2000).

Sources of heterogeneity within groups

We assumed that variation in effect size could be due to taxonomic grouping (i.e. closely related organisms may be more similar in effect size compared with more distant groups) or due to dose rate for each experiment. We used a step-wise partitioning technique *sensu* Gurevitch *et al.* (1992) to identify sources of within-group variation (Q_W) using taxonomic information. Therefore, we used a mixed effects model to compare mean effect sizes between taxonomic groups when enough comparisons (≥ 4) were available. We used a continuous random effects model to explore the relationship between effect size and hours of UVB radiation per day, total hours of UVB for each experiment, and dose when available. Several weighting functions are commonly used to assess irradiance and dosage levels. Weighting functions are calculated according to which specific wavelengths in the UVB band are most damaging to particular organisms. These weighting functions include erythemal (McKinlay & Diffey 1987), DNA (Setlow 1974) and plant (Caldwell 1971) action spectra. As dose estimates with different weighting functions are not comparable, each weighting function was considered separately.

Sensitivity analysis

For each analysis, including exploratory analyses, we used a form of sensitivity analysis to assess the influence of unusually large effect sizes on the analyses. We ranked each comparison by magnitude of effect size, removed each unusually large comparison step-wise, and re-ran each analysis. This procedure tests the influence of these large effect sizes on the conclusions of the analyses and the heterogeneity statistics.

Publication bias

For each analysis, we used several standard methods to identify potential publication bias ('file drawer problem', Rosenthal 1979). We generated normal quantile plots of standardized effect size against the standard normal distribution to visually assess bias (Wang & Bushman 1998; Rosenberg *et al.* 2000). We used Spearman's rank correlation test to formally test for publication bias. In addition, we calculated Rosenberg's failsafe number (Rosenberg 2005) to quantitatively assess the importance of potential publication bias to the outcome of our analyses. Rosenberg's failsafe number is the number of studies with an effect size of precisely zero necessary to change the results of an analysis from significant to nonsignificant. No evidence of publication bias was detected in normal quantile plots of standardized effect size (d) in either the survival analysis or the growth analysis, as the plots were relatively linear and all points fall within the CIs (Fig. S3). Spearman's rank correlation tests were nonsignificant for both survival ($R = 0.087$; $P = 0.42$) and growth ($R = -0.04$; $P = 0.81$), indicating no significant correlation between standardized effect size and sample size. Rosenberg's failsafe number was large for both the survival (227 comparisons) and growth (76 comparisons) analyses.

RESULTS

Effect of UVB radiation on survival

Ultraviolet-B radiation had a significant and large negative effect on survival in aquatic organisms (Fig. 1a). However, there were no differences in mean effect size between marine and freshwater organisms (Fig. 1b), field and laboratory experiments (Fig. 1c), trophic levels (Fig. 1d) or life history stages (Fig. 1e). With the exception of primary producers, UVB radiation had a large negative effect

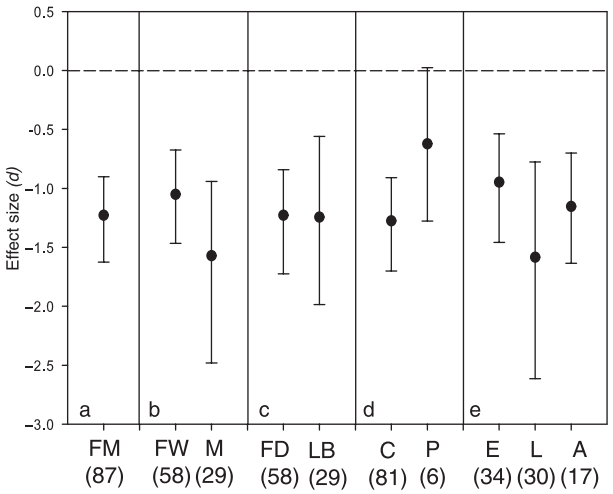

Figure 1 The effect of UV-B radiation on survival. The mean and 95% confidence interval is shown for each analysis. The number of comparisons used to calculate each mean is shown in parentheses. Confidence intervals that overlap the dashed line at zero are not significantly different from zero. FM, full model; FW, freshwater; M, marine; FD, field; LB, laboratory; C, consumer; P, primary producer; E, embryo; L, larva; A, adult.

Table 1 Heterogeneity statistics for each model in the survival analysis. Separate analyses were conducted to compare similarity in effect size between each group

Statistical model	d.f.	Q	P
Full model (no structure)	86	169.66	< 0.0001
Habitat type			
Between groups	1	2.01	0.16
Within groups	85	169.57	< 0.0001
Experimental venue			
Between groups	1	0.001	0.97
Within groups	85	168.23	< 0.0001
Trophic group			
Between groups	1	0.90	0.34
Within groups	85	168.16	< 0.0001
Developmental stage			
Between groups	2	2.45	0.29
Within groups	78	164.35	< 0.0001

($d_+ > -0.8$) in all groups (all effect size estimates were significantly different from zero). UVB radiation had a moderate effect ($d_+ = -0.6$) on primary producers that was not significantly different from zero.

In all models, significant within-group heterogeneity was observed (Table 1). Therefore, we used hierarchical structure (taxonomic groups) and dose rate in an attempt to partition variance. Our analyses were limited by the small number of taxonomic groups with more than four comparisons; however, no differences between taxonomic groups were detected and significant within-group heterogeneity persisted through all levels of taxonomic grouping (Table S3). Similarly, significant residual error was found in each model examining dose-rate variables (Table S4). Surprisingly, the relationship between dose-rate variables and effect size was negative in only two models (hours of UVB radiation per day and DNA-weighted dose estimates).

Effect of UVB radiation on growth

Ultraviolet-B radiation had a large negative effect on growth in aquatic organisms (Fig. 2a). No differences in growth were detected between habitats (Fig. 2b) or experimental venue (Fig. 2c). UVB radiation had a larger negative effect on primary producers than on consumers, but this trend was only marginally significant (Fig. 2d; $P = 0.057$; Table 2). However, the effects of UVB radiation on growth varied by life history stage (Fig. 2e; $P = 0.002$; Table 2). The effects of UVB radiation were larger in embryos than in larvae ($P < 0.0001$). No differences were detected between embryos and adults ($P = 0.19$) or between adults and larvae ($P = 0.019$; nonsignificant at $\alpha = 0.017$ after Bonferroni adjustment). The analysis included only four studies of

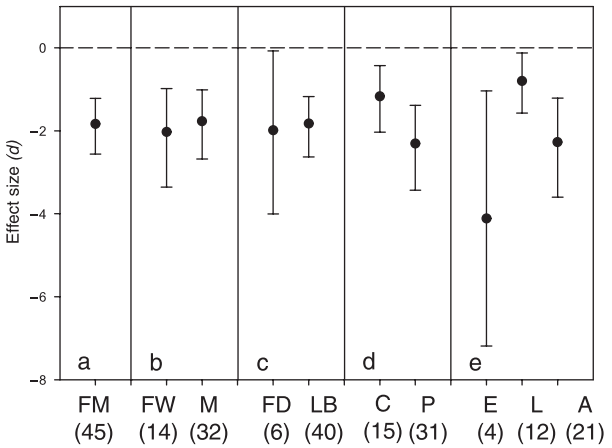

Figure 2 Effect of UV-B radiation on growth. The mean and 95% confidence interval is shown for each analysis. The number of comparisons used to calculate each mean is shown in parentheses. All means are significantly different from zero (95% confidence intervals do not overlap with the dashed line at zero). FM, full model; FW, freshwater; M, marine; FD, field; LB, laboratory; C, consumer; P, primary producer; E, embryo; L, larva; A, adult.

growth in embryos. The wide CIs around the effect size estimate for embryos are a direct result of one large negative effect size (−27.55). A significant difference between these groups remained after removal of this large value ($P = 0.02$). As in the survival analysis, all mean effect sizes in the growth analysis were moderate to large ($d_+ > -0.7$) and negative. Moreover, the mean effect size for every group was significantly different from zero.

Although the between-group heterogeneity was frequently nonsignificant, the within-group heterogeneity was large and significant in every model (Table 2). Similar to the survival analysis, we used taxonomic grouping and dose-rate variables to partition variance. UVB radiation had a larger effect on members of the kingdom Protozoa than on any other kingdom in this analysis (Fig. 3). However, significant heterogeneity within groups was still detected at the level of kingdom (Table S5). Further partitioning was limited by the number of comparisons within groups. Significant within-group heterogeneity persisted through all levels of taxonomic grouping (Table S5). The relationship between effect size and dose-rate variables was nonsignificant in all models except days of exposure (Table S6). Moreover, significant residual error persisted in all models except between dose and mean effect size (Table S6). Unfortunately, few studies reported dose and those that did used one of several possible weighting functions. Therefore, we are unable to fit different slopes using analysis of covariance models to assess the contribution of different taxonomic or other grouping variables on the dose–effect size relationship.

Table 2 Heterogeneity statistics for each model in the growth analysis. Separate analyses were conducted to compare similarity in effect size between each group

Statistical model	d.f.	Q	P
Full model (no structure)	45	104.42	< 0.0001
Habitat type			
Between groups	1	0.17	0.68
Within groups	44	100.74	< 0.0001
Experimental venue			
Between groups	1	0.039	0.84
Within groups	44	102.98	< 0.0001
Trophic group			
Between groups	1	3.61	0.057
Within groups	44	97.67	< 0.0001
Developmental stage			
Between groups	2	12.22	0.002
Within groups	34	79.82	< 0.0001

Sensitivity analyses

Weighted histograms of effect size are left-skewed due to some extreme negative values (Fig. 4). These values do not affect the overall normality of the data in the normal quantile plots (Fig. S3). These two types of plots reveal different types of patterns in the data. In a weighted histogram, the height of each bar reflects the combined weight of the studies within that class (Rosenberg *et al.* 2000). If the effect sizes are plotted as a simple frequency histogram, the left skew is greatly reduced (data not shown). Therefore, the apparent conflict between the normal quantile plots and the weighted histograms is a direct result of the weighting function. The unusually large effect sizes have very low weights compared to the smaller effect sizes, even if their frequency of occurrence is similar.

To test the robustness of our analyses against these extreme values, we removed each comparison with a large negative effect step-wise and re-ran each analysis. We began with the highest ranked effect size in each analysis and continued to remove the next largest effect size until Q was nonsignificant. Ten and eight comparisons were removed from the survival and growth analyses respectively. After removal of these values, the weighted histograms were essentially unimodal with the highest frequency around zero effect size (Fig. 5). Removing extreme values had no effect on the overall conclusions of the analyses: UVB radiation still had a large ($d_{++} = -0.88, -1.22$) effect on survival and growth respectively. In addition, heterogeneity in the full model was reduced to nonsignificance after removal of

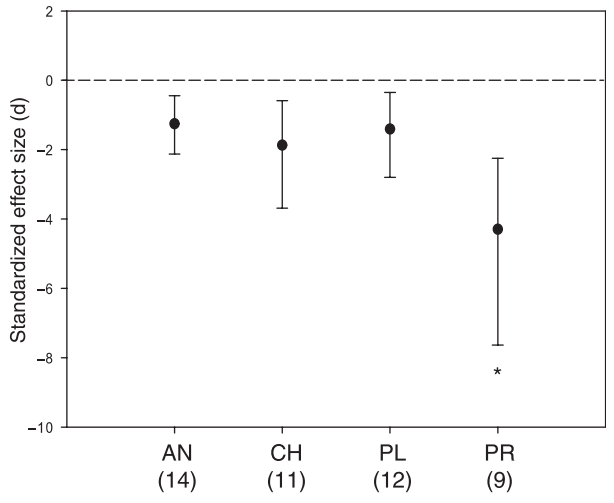

Figure 3 Effect of UV-B radiation on growth in each kingdom. The mean and 95% confidence interval is shown for each kingdom. The means are all significantly different from zero as none of the 95% confidence intervals overlap zero. UV-B radiation has a significantly larger negative effect on members of the kingdom Protozoa (asterisk). AN, Animalia; CH, Chromista; PL, Plantae; PR, Protozoa.

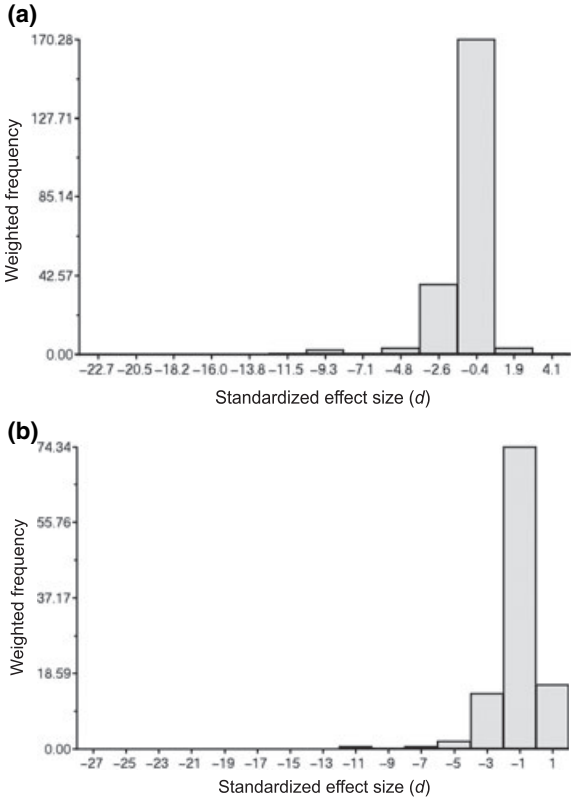

Figure 4 Weighted histogram of effect sizes for all comparisons in the survival analysis (a) and growth analysis (b). The height of each bar indicates the combined weight of effect sizes in each class. The distribution is left-skewed due to several extreme negative values with low weight.

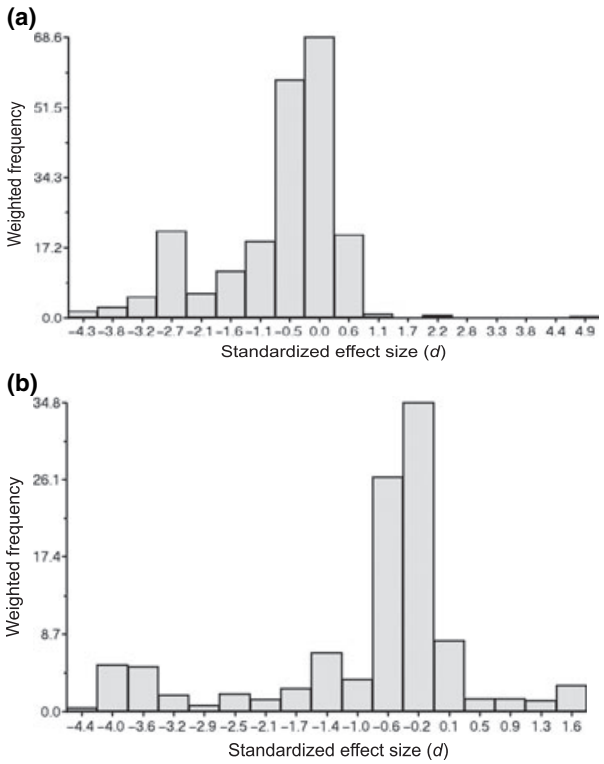

Figure 5 Weighted histogram of effect sizes after removal of effect sizes greater than 1 standard deviation from zero. The height of each bar indicates the combined weight of effect sizes in each class. The distribution of weighted effect sizes for the survival analysis (a) and growth analysis (b) are normal and show no evidence of publication bias.

these effect sizes ($Q = 85.33$, d.f. $= 73$, $P = 0.15$; $Q = 50.22$, d.f. $= 37$, $P = 0.07$) in the survival and growth analyses respectively.

Removal of the largest values step-wise had few effects on the conclusions of the exploratory analyses. Removal of the 10 largest effect sizes had no effect on the conclusions of the survival analyses. Heterogeneity was reduced to nonsignificance in all survival analyses (data not shown). In the growth analyses, removal of the eight largest effect sizes had no effect on the conclusions of the venue, habitat or life history stage exploratory analyses. The difference in growth between trophic groups moved from marginally significant to nonsignificant when the largest effect size was removed from the analysis. Heterogeneity was reduced to nonsignificance in all but the analysis of the effects of growth between life history stages.

DISCUSSION

Ultraviolet-B radiation had a large negative effect on both survival and growth in our analyses. Traditional reviews and syntheses of the effects of UVB on aquatic organisms generally suggest that the effects of UV vary widely among organisms (Siebeck *et al.* 1994; de Mora *et al.* 2000; Häder *et al.* 2003; Helbling & Zagarese 2003). This assertion reflects the patterns in the literature. A conventional 'vote-count' of the comparisons included in the analysis would conclude that UVB radiation has a limited effect on survival. Less than half (45%) of the original comparisons observed a significant effect of UVB radiation on survival. A vote-count of the effects of UVB radiation on growth would detect a negative effect, as approximately 60% of studies reported a significant effect on growth. These analyses demonstrate the potential for meta-analytic techniques to identify broad trends that may be obscured by variation and poor statistical power. Significance level depends on both the size of the measured effect and the sample size of each treatment (Gurevitch *et al.* 1992). Thus, two studies measuring the same effect may have different statistical outcomes simply due to different sample sizes.

Due to the large heterogeneity statistics in both the survival and growth analyses, it may be incorrect to conclude that the grand mean effect size plus the 95% CI is an accurate estimate of the true distribution of effects of UVB radiation in aquatic organisms (Hedges & Olkin 1985; Gurevitch *et al.* 1992). However, when we removed the largest effect sizes, the heterogeneity statistic moved to nonsignificance. Thus, it is possible that there were two distinct populations of effect sizes that we did not isolate using taxonomic groupings or dose–response variables.

To explore the heterogeneity further, we examined the details of each comparison with unusually large effect sizes to find commonalities between these comparisons that may indicate the source of the large effects. In the survival analyses, the large effect sizes were almost equally distributed across the groups (Table S1). All of the unusually large effect sizes were members of the kingdom Animalia (and therefore also classified as consumers in the trophic analysis), but this alone is not surprising given the paucity of comparisons in the other kingdoms (Table S1). The only striking similarity between these comparisons is that 9 of the 10 with the largest effect sizes also have extremely large variance (Table S1). In the growth analyses, seven of the eight unusually large effect sizes were laboratory studies. However, given that only six of the included comparisons were field studies, this was expected. All eight of these comparisons were primary producers. These eight comparisons represented members of all three phototrophic kingdoms (Table S2), but half of them were from the kingdom Protozoa. Similar to the survival analysis, all eight comparisons removed from the growth analyses had extremely large variance (Table S2). Thus, the majority of the comparisons with unusually large effect sizes in each analysis also had large variance, and therefore may have low

precision. Our estimates of variance were calculated using both sample size and the value of *d* for each comparison (Rosenberg *et al.* 2000). Samples with very large effect sizes and small sample sizes will therefore have large estimates of variance. However, small sample size alone did not always lead to a large effect size or a large variance.

Considering the general lack of commonality between these comparisons we could not isolate the potential cause of the heterogeneity. Moreover, we could not justify removing these comparisons from the analysis. Therefore, below we discuss the results from the full analyses (with the very large effects included), but cautiously interpret results that were altered by the removal of the large effect sizes. We believe that for the majority of the comparisons in these analyses, the estimate of mean effect size and the associated 95% CI is a reasonable approximation of the effect of UVB radiation on survival and growth in these organisms. Moreover, it is important to realize that the large significant heterogeneity observed in these models is driven by extremely large negative effects that may lie outside the expected distribution of effect sizes. These large effect sizes may be due to extreme experimental conditions or indicate that these organisms are particularly susceptible to damage from UVB radiation. More research into these organisms with larger sample sizes is necessary to explore the basis for the large effect sizes observed in these comparisons. However, the large negative effect of UV-B radiation on survival and growth persists with or without these unusually large effect size estimates.

Our analyses suggest that the magnitude of the effect varies among organisms, but the effect tends to be large and negative. The negative effect of UVB on both survival and growth was detected despite different habitat types, life history stages, trophic levels and diverse taxonomic groups.

No differences in survival or growth between marine and freshwater organisms were detected, suggesting that the magnitude of the effect of UVB radiation cannot be predicted by habitat type. The optical qualities of marine waters can be very different from freshwater habitats. The depth at which 10% of surface UVB can be detected can vary by more than 2 orders of magnitude between temperate lakes and clear ocean waters, with much higher attenuation in freshwater habitats (Díaz *et al.* 2000). Despite the potential difference in UVB penetration between these systems, we did not observe a difference in effect size between freshwater and marine habitats. It is possible that the UVB penetration in these two habitat types was similar as the majority of marine studies were conducted in coastal environments where terrestrial run-off and estuarine contributions increase the levels of DOC in near-shore waters (Kirk 1994).

Exposure of organisms to UVB in the laboratory rarely approximates natural environments. Of specific concern is the ratio of UVB to both UVA and PAR necessary for photorepair of DNA. In most laboratory experiments the UVB dose is closely monitored and applied, but the dose of UVA and PAR tends to be much lower than in natural systems (e.g. Ankley *et al.* 2000). Surprisingly, no difference in mean effect size between laboratory and field exposures was found in either the survival or growth analyses. We do not believe that the ratio of UVB to UVA and PAR is unimportant: rather, our analyses suggest that the overall effect of UVB is negative regardless of the spectral quantity or quality of available light.

The effects of UVB radiation may vary over developmental stages (e.g. Häkkinen *et al.* 2001; Altamirano *et al.* 2003; Hessen 2003). However, variation in survival at different life history stages may have little impact at the population or community levels. For example, some amphibian species may be especially sensitive to UVB in early life stages but this may not affect them at the population level (Vonesh & De la Cruz 2002). Regardless, in our analysis, survival under UVB radiation was lower than shielded controls in all life history stages. Furthermore, embryos tend to grow more slowly when exposed to UVB radiation as illustrated in our analysis. Hampered growth in embryos could be due to several factors. Most importantly, the rate of cellular division is generally higher in embryos compared with other life history stages and DNA repair may be limited during rapid divisions within an embryo (Epel *et al.* 1999). Thus, development could be slowed by a damaged genome. Alternatively, development may be delayed by time-intensive repair mechanisms (Epel *et al.* 1999). However, this result is ambiguous because of the relatively few (four) comparisons of growth in embryos. More research is needed on the effects of UVB on growth of embryos to clarify the relationship between life history stage and reduced growth resulting from UVB exposure. Regardless of the differences in inherent susceptibility between life history stages, embryos are generally nonmotile, so behavioural avoidance of UVB in natural systems is unlikely unless oviposition occurs in a shielded environment. Therefore, embryos may be exposed to high levels of UVB during development. In contrast, motile stages and mobile species may prevent damage by behaviourally avoiding UVB radiation (Banaszak 2003; Blaustein & Belden 2003). Later life history stages of animals and many species of phytoplankton actively select microhabitats that may reduce exposure to UVB radiation (Häder 1993). However, there may be a trade-off between exposure to warm sunlit areas with higher levels of PAR (optimal for photosynthesis and thermoregulation) and avoidance of areas with harmful levels of UVB (Hutchison & Duprè 1992; Häder 1993). Negative effects of reduced growth during early life history stages on lifetime fitness have been demonstrated in several taxa including insects (Moeur & Istock 1980), birds

(Sedinger *et al.* 1995) and amphibians (Semlitsch *et al.* 1988). These delayed life history effects are rarely explicitly incorporated into theoretical models of population and community dynamics, but are important to our understanding of how early environments and conditions affect population fluctuation in natural systems (Beckerman *et al.* 2002).

Previous reviews have suggested that primary producers, particularly phytoplankton, may be especially sensitive to UVB radiation (e.g. Häder 1993; Day & Neale 2002). In our analysis, no differences in survival were observed between trophic groups. In the survival analysis, the mean effect size in primary producers was smaller than in consumers and not significantly different from zero. Few studies have examined survival in primary producers and the wide CI may reflect the small sample size ($n = 6$) in our analysis. Clearly, more research into the effects of UVB on survival of primary producers is necessary to determine the importance of UVB on trophic interactions. Our growth analysis suggests that UVB radiation may affect primary producers more than consumers, although the trend was only marginally significant and disappeared when the very large effect sizes were removed from the analysis. This trend may be driven by the large negative effect of UVB on protozoans. However, more research into the effect of UVB radiation on growth in primary producers is needed to clarify this trend. In particular, more work on the effects of UVB radiation on protozoans is necessary. Of the nine comparisons in the kingdom Protozoa, seven were of dinoflagellates and eight of the nine were the work of one laboratory (Ekelund 1990; Ekelund 1991; Ekelund 1993). In mesocosm experiments with plankton communities, several studies reported a larger negative effect of UVB on phytoflagellates (protozoans) compared to diatoms (Villafañe *et al.* 1995; Hernando *et al.* 2006) but in other experiments the opposite trend was observed (Wängberg *et al.* 1996). Reduced growth of primary producers may lead to bottom-up control of these systems due to diminished food resources.

Previous reviews highlight the variation in susceptibility to UVB between organisms (de Mora *et al.* 2000; Helbling & Zagarese 2003). Our analyses demonstrate this variation in the distribution of effect sizes represented by mean and 95% CIs. Effect sizes in these analyses ranged from −27.5 to 5.20 (Tables S1 and S2). Although the overall effect was large and negative, individual species may be more susceptible to damage from UVB. Our random effects model allowed for a distribution of effect sizes and the estimates of pooled SD were relatively large (1.8262 and 2.6332 in the survival and growth analyses respectively). Varying resistance to damage from UVB may lead to shifts in diversity or richness in both freshwater and marine phytoplankton populations, as has been observed in zooplankton communities (Marinone *et al.* 2006). Community composition may shift to favour a microbial web over a heterotrophic web (e.g. Mostajir *et al.* 1999). These shifts in community composition, diversity or species richness in addition to the effects of UVB on dissolved carbon may alter the carbon dynamics in the oceans (Mostajir *et al.* 2000). The majority of experiments on community effects of UVB focus on one component of a natural community (i.e. phytoplankton community). Including more community components may reveal shifts in community structure that are not predicted based on sensitivity to UVB alone. For example, Bothwell *et al.* (1994) observed indirect positive effects of UVB radiation on algae due to a reduction in herbivory. The effects of UVB on communities may be transient. A recent study by Wahl *et al.* (2004) found no difference in diversity or biomass between marine benthic communities exposed to UVB and communities shielded from UVB after 12 weeks. More long-term experiments on communities are necessary to fully understand the effects of UVB radiation on diversity, richness and ecological function.

Although we predicted that the effects of UVB would vary along taxonomic groupings, significant heterogeneity persisted through all taxonomic levels. Partitioning variance using the level of kingdom was impossible in the survival analysis as the vast majority of comparisons in this analysis focused on members of the kingdom Animalia (80 of 86). Even within the kingdom Animalia, our attempts to partition variance through taxonomic structure were unsuccessful and significant heterogeneity persisted in each model. Similarly, significant heterogeneity persisted in every model in the growth analysis. This variation in effect size most likely reflects both intra- and interspecies variation in susceptibility to UVB radiation in addition to variation due to experimental conditions such as optical characteristics of water, timing of UVB exposure and dose rate.

In an attempt to quantify the relationship between experimental conditions and effect size we used dose and dose rate variables that included hours of UVB per day, total hours of UVB, days of UVB exposure and daily dose. In the survival analysis we were also able to include total erythemal dose (erythemal dose per day summed across all exposure days). We could not use optical characteristics in our analysis as most authors do not report these types of data (e.g. extinction coefficients). We predicted a relationship between dose and effect size, as many organisms respond to UVB with a dose–response curve (Damkaer *et al.* 1981; McNamara & Hill 1999; Ankley *et al.* 2002; Browman *et al.* 2003; Hessen 2003). In all cases the fit to the model was nonsignificant, suggesting that the relationship between dose-rate variables and effect size was weak in the survival analysis. In the growth analysis, the regression term was nonsignificant in all models except days of UVB exposure. Although the regression term was significant in the days of exposure regression model, the residual error term was

highly significant; thus, the overall fit to the model was poor. These analyses did not detect a strong relationship between dose-rate variables and effect size. Interspecific variation in conjunction with experimental variation may obscure the dose–effect size relationship in our analyses.

Broader impacts and conservation implications

To our knowledge, these analyses are the first quantitative evidence of the overall negative impact of UVB radiation on aquatic organisms. Traditional reviews of the effects of UVB radiation are unable to detect the broad patterns revealed by our meta-analyses. These reviews emphasize the variation between organisms, habitats, life history stages and trophic levels (e.g. Siebeck *et al.* 1994; de Mora *et al.* 2000; Häder *et al.* 2003; Helbling & Zagarese 2003). Our analyses captured this variation through the distribution of effect sizes, but also reveal a strong negative effect of UVB despite this variation. The dynamics of UVB exposure and resulting organismal damage is complex in natural systems. The effects of UVB in both freshwater and marine systems are modulated by many factors including seasonality of UVB dose, total ozone concentration in the stratosphere, cloudiness, local topography, DOC, organismal behaviour and repair mechanisms. These factors may vary widely between studies, habitats, developmental stage or species; however, these analyses emphasize the commonality of a negative effect of UVB radiation. The most striking and important result of these analyses is the consistency of the effect of UV regardless of other moderating variables within each study. These variables may have a large impact within a study, but when all the data were combined, the majority of comparisons showed a negative effect of UVB that was within the expected distribution of effect sizes. Moreover, those studies that did not fall within the expected distribution had larger (more negative) effect sizes. Our analyses highlight the importance of UVB radiation in both marine and freshwater organisms.

The response variables selected for these analyses are only two of the many possible effects of UVB radiation; therefore, it is likely that these analyses underestimate the potential effects of UVB in natural systems. For example, effects such as reduced photosynthetic rates, tissue damage and behavioural changes have been documented in many species (reviewed in Tevini 1993; de Mora *et al.* 2000; Helbling & Zagarese 2003). If UVB radiation has a negative effect on all these variables, the overall influence of UVB could be high in these systems. Moreover, predicted increases in acidification may reduce the DOC levels in freshwater systems, resulting in higher UVB exposure in these systems (Vinebrooke *et al.* 2004).

As a consequence of global environmental change, stressors such as UVB, chemical contaminants, drought, disease and acidification are increasingly common in natural systems. We did not include additional stressors in these analyses, but it is unlikely that a system would be exposed to only one stressor at a time. Environmental stressors such as UVB may interact with other environmental or biotic stressors and result in non-additive responses that are larger than predicted by each stressor individually (Vinebrooke *et al.* 2004). For example, UVB radiation acts synergistically with other stressors such as contaminants, disease and extreme thermal events (Kiesecker & Blaustein 1995; Häder *et al.* 2003; Pelletier *et al.* 2006). Alternatively, one stressor may have an antagonistic effect on other stressors, such that exposure to two stressors is less than additive (Christensen *et al.* 2006).

At the community level, differences in susceptibility to environmental stressors may vary between organisms, leading to unforeseen interactions between stressors on the community as a whole. For example, one species may be more susceptible to chemical contaminants and less susceptible to UVB radiation, while another species is less susceptible to chemical contaminants but more susceptible to UVB radiation. Because these two stressors may be found in the same habitat, the overall effect of the stressors may be greater than predicted considering each stressor alone. Exposure to multiple stressors may shift communities towards dominance by a few hardy species (Christensen *et al.* 2006). Synergisms among stressors are increasingly important in the face of global environmental change and must not be ignored when considering both the effects of UVB on a single species and the effects of UVB on entire communities and systems.

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REFERENCES

Adams, D.C., Gurevitch, J. & Rosenberg, M.S. (1997). Resampling tests for meta-analysis of ecological data. *Ecology*, 78, 1277–1283.

Altamirano, M., Flores-Moya, A. & Figueroa, F.L. (2003). Effects of UV radiation and temperature on growth of germlings of three species of *Fucus* (Phaeophyceae). *Aquatic Botany*, 75, 9–20.

Ankley, G.T., Tietge, J.E., Holocombe, G.W., DeFoe, D.L., Diamond, S.A., Jensen, K.M. *et al.* (2000). Effects of laboratory ultraviolet radiation and natural sunlight on survival and development of *Rana pipiens*. *Canadian Journal of Zoology*, 78, 1092–1100.

Ankley, G.T., Diamond, S.A., Tietge, J.E., Holocombe, G.W., Jensen, K.M., DeFoe, D.L. *et al.* (2002). Assessment of the risk

of solar ultraviolet radiation to amphibians: I. Dose-dependent induction of hindlimb malformations in the Northern Leopard Frog (*Rana pipiens*). *Environmental Science & Technology*, 36, 2853–2858.

Banaszak, A.T. (2003). Photoprotective physiological and biochemical responses of aquatic organisms. In: *UV Effects in Aquatic Organisms and Ecosystems* (eds Helbling, E.R. & Zagarese, H.). Royal Society of Chemistry, Cambridge, UK, pp. 329–356.

Beckerman, A., Benton, T.G., Ranta, E., Kaitala, V. & Lundberg, P. (2002). Population dynamic consequences of delayed life-history effects. *Trends in Ecology and Evolution*, 17, 263–269.

Belden, L.K., Wildy, E.K. & Blaustein, A.R. (2000). Growth, survival and behavior of larval long-toed salamanders (*Ambystoma macrodactylum*) exposed to ambient levels of UV-B radiation. *Journal of Zoology (London)*, 251, 473–479.

Blaustein, A.R. & Belden, L.K. (2003). Amphibian defenses against ultraviolet-B radiation. *Evolution & Development*, 5, 89–97.

Blaustein, A.R., Hoffman, P.D., Hokit, D.G., Kiesecker, J.M., Walls, S.C. & Hays, J.B. (1994). UV repair and resistance to solar UV-B in amphibian eggs: a link to population declines? *Proceedings of the National Academy of Sciences of the United States of America*, 91, 1791–1795.

Blaustein, A.R., Kiesecker, J.M., Chivers, D.P., Hokit, D.G., Marco, A., Belden, L.K. *et al.* (1998). Effects of ultraviolet radiation on amphibians: field experiments. *American Zoologist*, 38, 799–812.

Blaustein, A.R., Hatch, A.C., Belden, L.K., Scheessele, E. & Kiesecker, J.M. (2003). Global change: challenges facing amphibians. In: *Amphibian Conservation* (ed. Semlitsch, R.D.). Smithsonian Books, Washington, D.C., pp. 187–198.

Bothwell, M.L., Sherbort, D.M.J. & Pallock, C.M. (1994). Ecosystem response to solar ultraviolet-B radiation: influence of trophic level interactions. *Science*, 265, 97–100.

Browman, H.I., St-Pierre, J.F. & Kuhn, P. (2003). Dose and dose-rate dependency in the mortality response of *Calanus finmarchicus* embryos exposed to ultraviolet radiation. *Marine Ecology Progress Series*, 247, 297–302.

Buma, A.G.J., Boelen, P. & Jeffery, W.H. (2003). UVR-induced DNA damage in aquatic organisms. In: *UV Effects in Aquatic Organisms and Ecosystems* (eds Helbling, E.R. & Zagarese, H.). Royal Society of Chemistry, Cambridge, UK, pp. 291–327.

Caldwell, M.M. (1971). Solar UV irradiation and the growth and development of higher plants. *Photophysiology*, 6, 131–177.

Caldwell, M.M., Björn, L.O., Bornman, J.F., Flint, S.D., Kulandaivelu, G., Teramura, A.H. *et al.* (1998). Effects of increased solar ultraviolet radiation on terrestrial ecosystems. *Journal of Photochemistry and Photobiology. B, Biology*, 46, 40–52.

Charron, R.A., Fenwick, J.C., Lean, D.R.S. & Moon, T.W. (2000). Ultraviolet-B radiation effects on antioxidant status and survival in the zebrafish, *Brachydanio rerio*. *Photochemistry and Photobiology*, 72, 327–333.

Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J. & Turner, M.A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology*, 12, 2316–2322.

Cohen, J. (1969). *Statistical Power Analysis for the Behavioral Sciences*. Academic Press Inc., New York, NY.

Díaz, S.B., Morrow, J.H. & Booth, C.R. (2000). UV physics and optics. In: *The Effects of UV Radiation in the Marine Environment* (eds de Mora, S., Demers, S. & Vernet, M.). Cambridge University Press, Cambridge, UK, pp. 35–71.

Damkaer, D.M., Dey, D.B. & Heron, G.A. (1981). Dose/dose-rate responses of shrimp larvae to UV-B radiation. *Oecologia*, 48, 178–182.

Dattilio, A., Bracchini, L., Carlini, L., Loiselle, S. & Rossi, C. (2005). Estimate of the effects of ultraviolet radiation on the mortality of *Artemia franciscana* in naupliar and adult stages. *International Journal of Biometeorology*, 49, 388–395.

Day, T.A. & Neale, P.J. (2002). Effects of UV-B radiation on terrestrial and aquatic primary producers. *Annual Review of Ecology and Systematics*, 33, 371–396.

Ekelund, N.G.A. (1990). Effects of UV-B radiation on growth and motility of four phytoplankton species. *Physiologia Plantarum*, 78, 590–594.

Ekelund, N.G.A. (1991). The effects of UV-B radiation on dinoflagellates. *Journal of Plant Physiology*, 138, 274–278.

Ekelund, N.G.A. (1993). The effect of UV-B radiation and humic substances on growth and motility of the flagellate, *Euglena gracilis*. *Journal of Plankton Research*, 15, 715–722.

Epel, D., Hemela, K., Shick, M. & Patton, C. (1999). Development in the floating world: defenses of eggs and embryos against damage from UV radiation. *American Zoologist*, 39, 271–278.

Farman, J.C., Gardiner, B.G. & Shanklin, J.D. (1985). Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. *Nature*, 315, 207–210.

Gotelli, N.J. & Ellison, A.M. (2004). *A Primer of Ecological Statistics*. Sinauer Associates, Inc., Sunderland, MA.

Gurevitch, J. & Hedges, L.V. (1999). Statistical issues in ecological meta-analysis. *Ecology*, 80, 1142–1149.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992). A meta-analysis of competition in field experiments. *The American Naturalist*, 140, 539–572.

Gurevitch, J., Morrison, J.A. & Hedges, L.V. (2000). The interaction between competition and predation: a meta-analysis of field experiments. *The American Naturalist*, 155, 435–453.

Häder, D.-P. (1993). Effects of enhanced solar ultraviolet radiation on aquatic ecosystems. In: *UV-B Radiation and Ozone Depletion: Effects on Humans, Animals, Plants, Microorganisms, and Materials* (ed. Tevini, M.). Lewis Publishers, Boca Raton, FL, pp. 155–192.

Häder, D.-P., Kumar, H.D., Smith, R.C. & Worrest, R.C. (1998). Effects on aquatic ecosystems. *Journal of Photochemistry and Photobiology. B, Biology*, 46, 53–68.

Häder, D.-P., Kumar, H.D., Smith, R.C. & Worrest, R.C. (2003). Aquatic ecosystems: effects of solar ultraviolet radiation and interactions with other climatic change factors. *Photochemical & Photobiological Sciences*, 2, 39–50.

Häkkinen, J., Pasanen, S. & Kukkonen, J.V.K. (2001). The effects of solar UV-B radiation on embryonic mortality and development in three boreal anurans (*Rana temporaria*, *Rana arvalis* and *Bufo bufo*). *Chemosphere*, 44, 441–446.

Halac, S., Felip, M., Camarero, L., Sommaruga-Wögrath, S., Psenner, R., Catalan, J. *et al.* (1997). An in situ enclosure experiment to test the solar UVB impact on plankton in a high-altitude mountain lake. I. Lack of effect on phytoplankton species composition and growth. *Journal of Plankton Research*, 19, 1671–1686.

Han, T., Han, Y.-S., Kain, J.M. & Häder, D.P. (2003). Thallus differentiation of photosynthesis, growth, reproduction, and UV-B sensitivity in the green alga *Ulva pertusa* (Chlorophyceae). *Journal of Phycology*, 39, 712–721.

Hargreaves, B.R. (2003). Water column optics and penetration of UVR. In: *UV Effects in Aquatic Organisms and Ecosystems* (eds Helbling, E.R. & Zagarese, H.). Royal Society of Chemistry, Cambridge, UK, pp. 59–105.

Hedges, L.V. & Olkin, I. (1985). *Statistical Methods for Meta-Analysis*. Academic Press, Inc., Orlando, FL.

Helbling, E.W. & Zagarese, H. (eds) (2003). *UV Effects in Aquatic Organisms and Ecosystems*. Royal Society of Chemistry, Cambridge, UK.

Hernando, M., Schloss, I., Roy, S. & Ferreyra, G. (2006). Photoacclimation to long-term ultraviolet radiation exposure of natural sub-Antarctic phytoplankton communities: fixed surface incubations versus mixed mesocosms. *Photochemistry and Photobiology*, 82, 923–935.

Hessen, D.O. (2003). UVR and pelagic metazoans. In: *UV Effects in Aquatic Organisms and Ecosystems* (eds Helbling, E.R. & Zagarese, H.). Royal Society of Chemistry, Cambridge, UK, pp. 401–430.

Houghton, R.A. & Woodwell, G.M. (1989). Global climatic change. *Scientific American*, 260, 18–26.

Hutchison, V.H. & Duprè, R.K. (1992). Thermoregulation. In: *Environmental Physiology of the Amphibia* (eds Feder, M.E. & Burggren, W.W.). University of Chicago Press, Ltd, London, UK, pp. 206–249.

Karentz, D., Bothwell, M.L., Coffin, R.B., Hanson, A., Herndl, G.J., Kilham, S.S. *et al.* (1994). Impact of UV-B radiation on pelagic freshwater ecosystems: report of working group on bacteria and phytoplankton. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie*, 43, 31–69.

Kelner, A. (1949). Photoreactivation of ultraviolet-irradiated *Escherichia coli*, with special reference to the dose-reduction principle and to ultraviolet-induced mutation. *Journal of Bacteriology*, 58, 511–522.

Kerr, J.B. & McElroy, C.T. (1993). Evidence for large upward trends of ultraviolet-B radiation linked to ozone depletion. *Science*, 262, 1032–1034.

Kiesecker, J.M. & Blaustein, A.R. (1995). Synergism between UV-B radiation and a pathogen magnifies amphibian embryo mortality in nature. *Proceedings of the National Academy of Sciences of the United States of America*, 92, 11049–11052.

Kirk, J.T.O. (1994). Optics of UV-B radiation in natural waters. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie*, 43, 1–16.

Leech, D.M. & Johnsen, S. (2003). Behavioral responses–UR avoidance and vision. In: *UV Effects in Aquatic Organisms and Ecosystems* (eds Helbling, E.R. & Zagarese, H.). Royal Society of Chemistry, Cambridge, UK, pp. 455–481.

van der Leun, J.C. & de Gruijl, F.R. (1993). Influences of ozone depletion on human and animal health. In: *UV-B Radiation and Ozone Depletion: Effects on Humans, Animals, Plants, Microorganisms, and Materials* (ed. Tevini, M.). Lewis Publishers, Boca Raton, FL, pp. 95–123.

Litchman, E. & Neale, P.J. (2005). UV effects on photosynthesis, growth and acclimation of an estuarine diatom and cryptomonad. *Marine Ecology Progress Series*, 300, 53–62.

Madronich, S. (1993). UV radiation in the natural and perturbed atmosphere. In: *UV-B Radiation and Ozone Depletion: Effects on Humans, Animals, Plants, Microorganisms, and Materials* (ed. Tevini, M.). Lewis Publishers, Boca Raton, FL, pp. 17–69.

Madronich, S. (1994). Increases in biologically damaging UV-B radiation due to stratospheric ozone reductions: a brief review. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie*, 43, 17–30.

Madronich, S., McKenzie, R.L., Björn, L.O. & Caldwell, M.M. (1998). Changes in biologically active ultraviolet radiation reaching the Earth's surface. *Journal of Photochemistry and Photobiology. B, Biology*, 46, 5–19.

Marinone, M.C., Marque, S.M., Suárez, D.A., Diéguez, M.d.C., Pérez, P., De Los Ríos, P. *et al.* (2006). UV radiation as a potential driving force for zooplankton community structure in Patagonian lakes. *Photochemistry and Photobiology*, 82, 962–971.

McKinlay, A.F. & Diffey, B.L. (1987). A reference action spectrum for ultraviolet induced erythema in human skin. *CIE Journal*, 6, 17–22.

McNamara, A.E. & Hill, W.R. (1999). Effects of UV-B dose and irradiance: comparison among grazers. *Journal of the North American Benthological Society*, 18, 370–380.

Moeur, J.E. & Istock, C.A. (1980). Ecology and evolution of the pitcher-plant mosquito. *The Journal of Animal Ecology*, 49, 775–792.

Molina, M.J. & Rowland, F.S. (1974). Stratospheric sink for chlorofluromethanes: chlorine atom-catalyzed destruction of ozone. *Nature*, 249, 810–812.

de Mora, S., Demers, S. & Vernet, M. (eds) (2000). *The Effects of UV Radiation in the Marine Environment. Cambridge Environmental Chemistry Series: 10*. Cambridge University Press, Cambridge, UK.

Mostajir, B., Demers, S., de Mora, S., Belzile, C., Chanut, J.-P., Gosselin, M. *et al.* (1999). Experimental test of the effect of ultraviolet-B radiation in a planktonic community. *Limnology and Oceanography*, 44, 586–596.

Mostajir, B.J., Demers, S., de Mora, S.J., Bukata, R.P. & Jerome, J.H. (2000). Implications of UV radiation for the food web structure and consequences on the carbon flow. In: *The Effects of UV Radiation in the Marine Environment* (eds de Mora, S., Demers, S. & Vernet, M.). Cambridge University Press, Cambridge, UK, pp. 310–320.

Pelletier, E., Sargian, P., Payet, J. & Demers, S. (2006). Ecotoxicological effects of combined UVB and organic contaminants in coastal waters: a review. *Photochemistry and Photobiology*, 82, 981–993.

Rafaelli, D. 2004. How extinction patterns affect ecosystems. *Science*, 306, 1141–1142.

Roleda, M.Y., Hanelt, D., Kräbs, G. & Wiencke, C. (2004a). Morphology, growth, photosynthesis and pigments in *Laminaria ochroleuca* (Laminariales, Phaeophyta) under ultraviolet radiation. *Phycologia*, 43, 603–613.

Roleda, M.Y., de Poll, W.H., Hanelt, D. & Wiencke, C. (2004b). PAR and UVBR effects on photosynthesis, viability, growth and DNA in different life history stages of two coexisting Gigartinales: implications for recruitment and zonation pattern. *Marine Ecology Progress Series*, 281, 37–50.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57–60.

Rosenberg, M.S. (2005). The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, 59, 464–468.

Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000). *MetaWin: Statistical Software for Meta-Analysis*, Version 2.0. Sinauer Associates, Sunderland, MA.

Rosenthal, R. (1979). The 'file drawer problem' and tolerance for null results. *Psychological Bulletin*, 86, 638–641.

Salo, H.M., Jokinen, I., Markkula, S.E. & Aaltonen, T.M. (2000). Ultraviolet B irradiation modulates the immune system of fish (*Rutilus rutilus*, Cyprinidae) II: blood. *Photochemistry and Photobiology*, 71, 65–70.

Sancar, A. & Sancar, G.B. (1988). DNA repair enzymes. *Annual Review of Biochemistry*, 57, 29–67.

Scully, N.M. & Lean, D.R.S. (1994). The attenuation of ultraviolet radiation in temperate lakes. *Arch. Hydrobiol. Beih.*, 43, 135–144.

Searles, P.S., Flint, S.D. & Caldwell, M.M. (2001). A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia*, 127, 1–10.

Sedinger, J.S., Flint, P.L. & Lindberg, M.S. (1995). Environmental influence on life-history traits: growth, survival, and fecundity in Black Brandt (*Branta bernicla*). *Ecology*, 76, 2404–2414.

Semlitsch, R.D., Scott, D.E. & Pechmann, J.H.K. (1988). Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology*, 69, 184–192.

Setlow, R.B. (1974). The wavelengths in sunlight effective in producing skin cancer: a theoretical analysis. *Proceedings of the National Academy of Sciences of the United States of America*, 71, 3363–3366.

Siebeck, O., Vail, T.L., Williamson, C.E., Vetter, R., Hessen, D., Zagarese, H. *et al.* (1994). Impact of UV-B radiation on zooplankton and fish in pelagic freshwater ecosystems. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, 43, 101–114.

Solomon, S. (1999). Stratospheric ozone depletion: a review of concepts and history. *Reviews of Geophysics*, 37, 275–316.

Solomon, S. (2004). The hole truth: What's news (and what's not) about the ozone hole. *Nature*, 427, 289–291.

Tevini, M. (ed.) (1993). Molecular biological effects of ultraviolet radiation. In: *UV-B Radiation and Ozone Depletion: Effects on Humans, Animals, Plants, Microorganisms, and Materials*. Lewis Publishers, Boca Raton, FL, pp. 1–15.

Villafañe, V.E., Helbling, E.W., Holm-Hansen, O. & Chalker, B.E. (1995). Acclimatization of Antarctic natural phytoplankton assemblages when exposed to solar ultraviolet radiation. *Journal of Plankton Research*, 17, 2295–2306.

Villafañe, V.E., Sundbäck, K., Figueroa, F.L. & Helbling, E.W. (2003). Photosynthesis in the aquatic environment as affected by UVR. In: *UV Effects in Aquatic Organisms and Ecosystems* (eds Helbling, E.R. & Zagarese, H.). Royal Society of Chemistry, Cambridge, UK, pp. 357–397.

Vinebrooke, R.D., Cottingham, K.L., Norberg, J., Scheffer, M., Dodson, S.I., Maberly, S.C. *et al.* (2004). Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos*, 104, 451–457.

Vonesh, J.R. & De la Cruz, O. (2002). Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia*, 133, 325–333.

Wahl, M., Molis, M., Davis, A., Dobretsov, S., Dürr, S.T., Johansson, J. *et al.* (2004). UV effects that come and go: a global comparison of marine benthic community level impacts. *Global Change Biology*, 10, 1962–1972.

Wang, M.C. & Bushman, B.J. (1998). Using the normal quantile plot to explore meta-analytic data sets. *Psychological Methods*, 3, 46–54.

Wängberg, S.-Å., Selmer, J.-S. & Gustavson, K. (1996). Effects of UV-B radiation on biomass and composition in marine phytoplankton communities. *Scientia Marina*, 60, 81–88.

Williamson, C.E. (1995). What role does UV-B radiation play in freshwater ecosystems? *Limnology and Oceanography*, 40, 386–392.

Williamson, C.E., Metgar, S.L., Lovera, P.A. & Moeller, R.E. (1997). Solar ultraviolet radiation and the spawning habitat of Yellow Perch, *Perca flavescens*. *Ecological Applications*, 7, 1017–1023.

Zepp, R.G. (2003). Solar UVR and aquatic cycles. In: *UV Effects in Aquatic Organisms and Ecosystems* (eds Helbling, E.R. & Zagarese, H.). Royal Society of Chemistry, Cambridge, UK, pp. 137–183.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Effect of UVB on survival (lnR).
Figure S2 Effect of UVB on growth (lnR).
Figure S3 Normal quantile plots.
Table S1 Summary information for survival analysis
Table S2 Summary information for growth analysis
Table S3 Taxonomic group variation in survival analysis
Table S4 Dose-rate variable variation in survival analysis
Table S5 Taxonomic group variation in growth analysis
Table S6 Dose-rate variable variation in growth analysis
Appendix S1 Criteria for inclusion of studies

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