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Responses of tropical plankton communities from the Mexican Caribbean to solar ultraviolet radiation exposure and increased temperature

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ABSTRACT

The aim of this study was to evaluate the effects of UVR on growth and taxonomic composition of tropical plankton communities in a scenario of increased temperature and ultraviolet radiation. Water samples were collected from a reef lagoon in the Mexican Caribbean (20.5° N, 86.5° W) during July 2010 and grown for 16 days in microcosms under two natural radiation treatments: a) PAB (PAR + UV-A + UV-B, 280–700 nm) and, b) P, (PAR, 400–700 nm) and two temperature conditions: a) ambient (28 °C), and, b) increased (ambient + 3 °C). A differential factorial response of the studied variables among the main taxonomic groups and more frequent species was found. The biomass of dinoflagellates and colorless plankton was negatively affected by UVR while the increased temperature had negative effects on diatom biomass and cell abundance. During the experimental period there were changes in the contribution of each taxonomic group. At ambient temperature there was a shift from a flagellate- to a diatom-dominated community; whereas at increased temperature diatoms co-dominated with flagellates. UVR exposure decreased the contribution of naked dinoflagellates (>20 μm) and cryptophytes. On the other hand, the most frequent diatom, *Cylindrotheca closterium* was negatively affected at increased temperature, while small chlorophytes (<10 μm), which were one of the dominant groups of flagellates, contributed significantly to the biomass at increased temperature at the end of the experiment. Synergistic effects of UVR and temperature were only detected at the species level in large diatoms (>20 μm; e.g. *Leptocylindrus* sp. and *Amphora* sp.) and in cryptophytes (>10 μm). Our results suggest that planktonic assemblages from the Mexican Caribbean are generally well-adapted to the high UVR fluxes and temperature with some species being positively influenced by increased temperature. However there are exceptions with some species being negatively affected by UVR, increased temperature or the combination of both factors. Therefore, our results indicate that under the high radiation conditions of tropical oceans, changes in community structure in terms of taxonomic composition and size distribution would occur in a scenario of global climate change.

1. Introduction

Global climate change is a complex phenomenon that involves alterations in multiple physical variables such as temperature, pH and ultraviolet-B radiation (UV-B, 280–315 nm) (Houghton et al., 2001). These variables are influenced by anthropogenic factors including fossil fuel combustion, which generates green-house gases that result in increased sea-surface temperatures (IPCC, 2007; Stott and Kettleborough, 2002), and the acidification of aquatic systems (Doney et al., 2008). In addition, the release of ozone-depleting substances such as chlorofluorocarbons (CFCs) and hydrofluorocarbons (HCFCs) has resulted in increased levels of UV-B (Staehelin et al., 2001).

Sea surface temperature, has already been observed to increase worldwide (Levitus et al., 2000; Roemmich and Gilson, 2009), including tropical areas (Diaz and Graham, 1996; Johnson and Xie, 2010). Actually, the predictions made by the Intergovernmental Panel on Climate Change (IPCC, 2007) indicate that the surface temperature could increase ~3 °C by the end of the century due to global warming. In a short-term context, a temperature increase was detected as a pulse of short duration (about 10 days), reaching up to 3 °C above the monthly average of summer seawater temperatures in a tropical setting (Banaszak et al., 2003).

Some studies have found that increased seawater temperature is beneficial for phytoplankton resulting in higher photosynthetic performance as compared to samples exposed to control temperatures

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(Halac et al., 2010; Lassen et al., 2010; Sobrino and Neale, 2007). However, a decrease in phytoplankton biomass, especially due to a decline in large diatoms, associated with global warming has also been reported (Lewandowska and Sommer, 2010). As has been demonstrated by several studies, warmer conditions benefit the growth of smaller species (Daufresne et al., 2009; Winder et al., 2009) even though the total phytoplankton biomass is reduced due to the decrease in large species.

The increased levels of UV-B in the Polar Regions and some temperate latitudes have stimulated research on the impact of UVR on natural phytoplankton communities. These effects include decreased cell abundance and growth rates in temperate marine communities (Marcoval et al., 2008; Nilawati et al., 1997). Other studies in marine environments, however, did not find such effects (Roy et al., 2006; Wängberg et al., 1999; Whitehead et al., 2000). The tropical areas normally receive higher fluxes of ultraviolet radiation (UVR, 280–400 nm) than mid and high latitudes due to their naturally thinner ozone layer and the more direct path of solar radiation through the atmosphere (Madronich, 1993). Therefore, phytoplankton are likely adapted to the high natural radiation levels, which may partially explain the lower sensitivity of tropical species in comparison to polar species to natural UVR (Helbling et al., 1992). Due to the increment of sea-surface temperatures and the potential negative effects of natural UVR exposure, some studies have highlighted the importance of evaluating the combined impact of UVR and temperature on organisms, because elevated temperatures can alter responses to UVR and thus can affect the prediction of the responses of aquatic ecosystems to future climate change scenarios (MacFadyen et al., 2004; Williamson et al., 2002). Even though the combination of UVR and increased temperature has been known to affect phytoplankton physiology (Davison, 1991; Halac et al., 2010; Sobrino and Neale, 2007), and taxonomic composition (Rae and Vincent, 1998; Xenopoulos et al., 2009), there are only few studies that assess both factors using natural communities, as compared with the evaluation of each variable separately. Some studies have reported a positive effect of combined UVR and temperature on the growth of phytoplankton communities demonstrating greater growth rates at higher temperatures under solar exposure (Doyle et al., 2005; Rae and Vincent, 1998). However, these responses are quite variable depending on the size of the species and on the taxonomic groups involved. Hence, community structure and taxonomic composition is greatly affected by the UVR–temperature interaction (Lionard et al., 2012; Thyssen et al., 2011).

Since UVR and temperature tolerance is species-specific, the community structure could change due to the differential sensitivity towards these variables. Moreover, some tropical species such as corals are already living at the upper limit of their temperature tolerance (Banaszak and Lesser, 2009), therefore, any increment in the sea surface temperature could affect these and other tropical species negatively. Thus we designed our study to evaluate the responses of tropical phytoplankton communities to the combined effects of increased temperature and UVR on growth, biomass and taxonomic composition. Our working hypothesis was that in tropical aquatic ecosystems increased temperature (as expected in a scenario of global climate change) will enhance the UVR-inhibition of growth, changing the community structure towards small acclimated cells. The experimental approach was to expose natural plankton communities to solar radiation (with and without UVR) for 16 days under ambient and increased temperature treatments and to evaluate growth, biomass and taxonomic composition throughout the experimental period.

2. Materials and methods

2.1. Sample collection and handling

The research described here was carried out at Puerto Morelos (20° 51′ N; 86° 55′ W) located in the Mexican Caribbean. Natural surface water samples were collected from the reef lagoon at the end of the pier belonging to the Universidad Nacional Autónoma de México (UNAM) in the Puerto Morelos National Reef Park using an acid-washed (1 N HCl) bucket. The samples were put into two 80 l acid-washed carboys and transported under low light conditions to the laboratory within 30 min. To screen out large zooplankton, the whole sample was filtered through 100 μm pore size mesh (Nitex®). Pilot studies indicated that when natural seawater was incubated in microcosms, there was no detectable plankton growth (data not shown), presumably due to the low nutrient concentrations (Rodríguez-Martínez et al., 2010). Therefore, for the experiment described here, nutrients were added to all samples prior to the start of the experiment to induce plankton growth. Macronutrients (NO_3^-, PO_4^{3-} and SiO_3^{2-}) at concentrations similar to f/2 medium (Guillard and Ryther, 1962) were added to the entire sample at 0.1% (v:v), mixed well and dispensed into 8 UVR-transparent (81% transmission at 280 nm) bags (20 l capacity) functioning as microcosms. As the experiment progressed, and after 6 days, a pulse of trace metals (same as that found in f/2 medium and at a total concentration of 0.1%, v:v) was added to all bags. The addition of nutrients in these experiments attempted to simulate not only the increased eutrophication observed in nearby areas due to intense tourism (van Tussenbroek, 2011) but also an increased input of terrestrial material related to increasing precipitation (Rodríguez-Martínez et al., 2010).

2.2. Exposure experiment

The experiment was carried out from July 14th to 29th 2010 (Julian days 195 to 210), with a pilot study undertaken previously, using 5 l bags that yielded similar results to those presented here (data not shown). Duplicate uncovered microcosms received PAR + UV-A + UV-B (PAB treatment; 280–700 nm) whereas another set of microcosms were wrapped with an Ultraphan filter (UV Opak, Digefra, Germany) and thus received PAR only (P treatment; 400–700 nm). A set of 4 microcosms (2 PAB and 2 P) were placed into each of two water tanks that measured 1.60 m in diameter × 45 cm high. One tank was maintained at 28 °C, which was the temperature measured in the water column at the time of sampling (ambient temperature or control), and the other tank was maintained at 31 °C (increased temperature). The temperature was maintained by a flow-through, water-bath system from two different sources. To maintain the microcosm at control temperatures, subterranean water at 25 °C was pumped from 90 m depth and because it was stored in tanks prior to its distribution into the aquarium system it heated by solar radiation to 28 °C. To maintain the other microcosm at 31 °C, seawater at 28 °C was pumped from the reef lagoon at a 4 m depth and because it was stored in tanks prior to its distribution into the aquarium system it heated by solar radiation to 31 °C. The temperature in both microcosms was monitored continuously by data loggers and several times daily by hand-held digital thermometers. To minimize the light gradient, the microcosms were placed in a horizontal plane, such that the surface area of the samples exposed was ~50 × 25 cm with a depth of 15 cm. Furthermore, samples were manually shaken once an hour during the day to avoid cell sedimentation. Gas exchange was promoted by injection of air using a syringe attached to plastic tubing inserted into the center of each microcosm. This system was also used for sampling.

2.3. Identification and quantification of cells and estimation of biomass

At the beginning of the experiment and then every other day, 50 ml of sample was taken from each microcosm and fixed in buffered formalin (0.4% final concentration, v:v). Twenty ml of each plankton sample was allowed to settle for 24 h using a graduated cylinder (LeGresley and McDermott, 2010). After settling, the supernatant was carefully removed until approximately 5% of the total volume was left. The remaining volume was well mixed and then dispensed into a Fuchs–Rosenthal chamber (Marienfeld, Germany) for quantification

and identification. A drop of Rose Bengal was added to each sample to better distinguish between organic material and detritus (Villafañe and Reid, 1995). Duplicate samples from each treatment were observed with a compound microscope (Zeiss model D-7082, Germany) using 200× magnification for microplankton cells (>20 μm) and 400× magnification for pico-nanoplankton (<20 μm). Species identification was made using Tomas (1997). To be considered a representative sample at least 100 cells of each of the most common species had to be present. The biovolume of each plankton species was estimated by shape assimilation to known geometric forms according to Hillebrand et al. (1999) and by measuring the main cell dimensions of 10 (in the case of the less frequent species) to 50 cells per species (in the case of the more frequent species). If size differences were observed within a species, the individuals of that species were divided into cell size classes to evaluate their volume more accurately. The calculated biovolumes had variation coefficients that were <10% within each measured species. From those biovolumes, biomass (as autotrophic carbon concentration) was estimated using the equations of Menden-Deuer and Lessard (2000).

2.4. Solar radiation and temperature measurements

PAR irradiance was measured for a 1 min period every 5 min throughout the experimental period using a cosine-corrected light sensor (LI-192, Li-Cor, USA) installed on a roof at a height of 4 m and attached to a data logger (LI-1400, Li-Cor). UVR was estimated with the STAR program (Ruggaber et al., 1994) using the PAR data. This model is extensively used and its output gives very good estimates of solar UVR as determined in previous studies (Buma et al., 2009). The water temperature in the center of each tank was registered using underwater data loggers (HOBO, USA) with a measurement frequency of one datum every 15 min.

2.5. Statistical and data analysis

The growth of the main groups was determined from both measurements of cellular abundance and estimations of carbon to take into account the changes in the size distribution that affect biomass but not cell abundance.

Growth rates were calculated as follows:

$$\mu = \ln(N_2 - N_1)/(t_2 - t_1) \quad (1)$$

where $(N_2–N_1)$ is the cell abundance or carbon content during the exponential growth phase and $(t_2–t_1)$ is the duration of the phase.

Data are expressed as the mean and half medium range of duplicate samples for both radiation and temperature treatments. To determine differences among treatments a significance level (α) of 0.05 was used for all comparisons (Zar, 1984). A one-way ANOVA test was used to establish if there existed differences in daily cell abundance or biomass and growth rates between radiation and temperature treatments, while a one-way repeated measures ANOVA was applied for testing the increase in cell abundance and/or biomass as the experiment progressed. A two-way ANOVA test was used to determine interactions between the two factors, radiation and temperature.

3. Results

3.1. Environmental conditions

In general, PAR (Fig. 1A) and UVR (Fig. 1B) irradiances were rather similar throughout the experiment with maxima ranging from 416 to 496 W m^{-2} (1913 to 2281 μmol photons m^{-2} s^{-1}) in the PAR and from 54 to 64 W m^{-2} in the UVR wavebands, with the exception of July 26th (Julian day 207) when, due to cloud cover and rain, PAR and UVR maximal irradiances decreased to 275 and 35 W m^{-2}, respectively. Temperatures inside the water tanks during the experiment were homogenous (data not shown). Maximum temperature fluctuations during each exposure day were approximately ± 1.3 °C with the exception of July 16th (Julian day 197) when the variation inside the ambient temperature tank was ±1.8 °C. Throughout the experiment the temperature fluctuations with respect to the maximum values were <17% and <13% in the ambient and increased temperature tanks, respectively.

3.2. Plankton community growth

The initial plankton community was characterized by four main groups: diatoms (mainly pennates), dinoflagellates, flagellates (including chlorophytes, cryptophytes and unidentified autotrophic flagellates) and colorless plankton (mainly heterotrophic dinoflagellates and flagellates). A few colonial cyanobacteria species were found in low abundance, therefore they were not considered in the calculation of total biomass and cell concentration. The growth of the four groups, estimated using biomass throughout the experiment, is presented in Fig. 2 and Table 1. There were no interactive effects ($p > 0.05$) between radiation and temperature treatments on the growth rates of any of the four groups. There were, however, significantly higher ($p < 0.05$) growth rates in the P treatment at 28 °C, as compared to PAB, of dinoflagellates and colorless plankton (Fig. 2C, G, Table 1), while no differences were observed in diatoms and flagellates at the same temperature. In the case of the increased temperature treatment, there were no significant effects of radiation in any of the groups. In relation to the temperature effect, there were significant decreases in both the growth rates and biomass attained by diatoms (both PAB and P treatments) at increased temperature (Fig. 2A, B, Table 1). Colorless plankton also showed a significant decrease in growth rate at increased temperature (as compared to the control; $p < 0.05$) in samples exposed only to PAR (Fig. 2G, H, Table 1). Growth rate data, based on cell abundance (Table 2), also indicated the significant ($p < 0.05$) negative impact of increased temperature for diatoms (both PAB and P treatments), flagellates (PAB treatment) and colorless plankton (P treatment).

3.3. Plankton community composition

3.3.1. Contribution of the main groups

The contribution of the main groups in the ambient and increased temperature treatments, based on biomass and abundance, is shown in Figs. 3 and 4, respectively. The relative contribution of the main groups to the total biomass throughout the experiment was variable

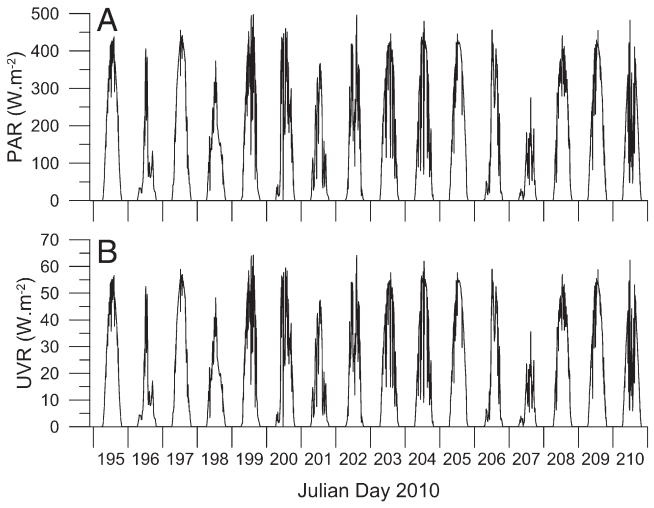

Fig. 1. PAR (A) and UVR irradiances (B) (in W m^{-2}) during the experimental period from Julian days 195 to 210 (July 14th to 29th 2010).

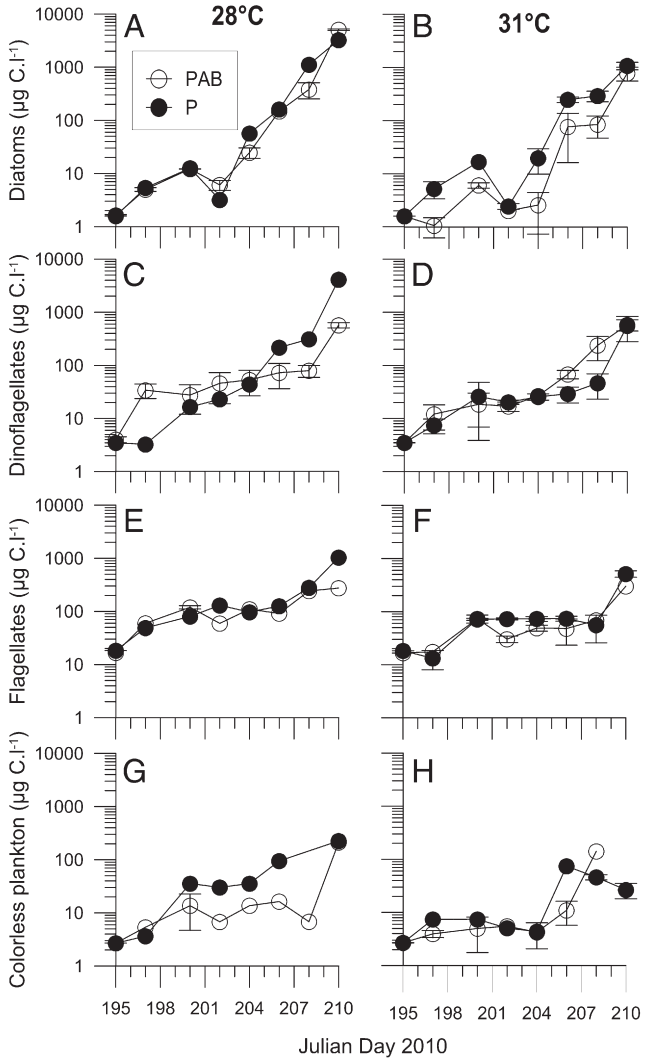

Fig. 2. Biomass (in µg C l^{-1}) of diatoms (A, B), autotrophic dinoflagellates (C, D), autotrophic flagellates (E, F) and colorless plankton (heterotrophic dinoflagellates and flagellates; G, H) in natural seawater samples exposed to solar radiation. Samples were exposed to two temperatures: 28 °C (A, C, E, G) and 31 °C (B, D, F, H) and two radiation treatments: PAB and P. The vertical lines on the symbols indicate the half mean range.

depending on the radiation and temperature treatments. However, a general trend of increased diatom dominance over time, with a concomitant decrease in flagellates was observed. This trend of diatom dominance was such that at the control temperature their contribution to biomass increased significantly from the initial value of ca. 7%, to 40% in the P treatment and 80% in the PAB treatment (Fig. 3A). Similar (PAB treatment) or smaller (P treatment) increases were observed in the increased temperature microcosms, with values reaching ca. 50% of the biomass (Fig. 3B). Flagellates were dominant at the beginning of the experiment accounting for ca. 70% of the total biomass (Fig. 3), but their share of the biomass decreased to ca. 15% in the P treatment and 5% in the PAB treatment at 28 °C (Fig. 3A). At the increased temperature, their share of the biomass at the end of the experiment accounted for ca. 20% in both the P and PAB treatments (Fig. 3B). Dinoflagellates were less abundant than the other two groups and their contribution to community biomass was rather constant and did not exceed 30%, with the exception of the P treatment at 28 °C; when by the end of the experiment they reached 48% of the total biomass (Fig. 3A). Colorless plankton had a very low contribution to biomass (ca. 5%).

In general, similar patterns as those described based on biomass were observed when the contribution of the main groups to cell abundance was examined (Fig. 4). The diatom allocation to total cell abundance was ca. 10% at the beginning of the experiment, increasing to 55% and 80% in the P and PAB treatments at 28 °C, respectively, by the end of the experiment (Fig. 4A). At increased temperature (Fig. 4B) the abundance share at the end of the experiment was 38% and 42% in the P and PAB treatments, respectively. Flagellates contributed 80% of the total abundance at the beginning of the experiment, whereas they accounted for ~20 and 50% of the abundances at 28 °C and 31 °C, respectively, after exposure (Fig. 4A, B). The contribution of dinoflagellates to the total abundance was low throughout the experiment (ca. 10%), as was that of colorless plankton (ca. 5%).

3.3.2. Species succession

The succession of the most abundant species of diatoms, dinoflagellates and flagellates is shown in Fig. 5. The abundances described in this figure correspond to the control conditions (i.e., full solar radiation or PAB treatment and ambient temperature at 28 °C) whereas the changes due to UVR exclusion or increased temperature are addressed in the section that follows. The most abundant species at the beginning of the experiment, in the taxonomic groups considered here, were the diatoms *Cylindrotheca closterium* (Ehrenberg) Reimann & J.C. Lewin, and naviculoid cells (Fig. 5A), unidentified naked dinoflagellates (<20 µm) and colorless dinoflagellates (Fig. 5C), unidentified chlorophytes (Fig. 5E), colorless flagellates and cryptophytes (Fig. 5F). Some of these most abundant species (e.g., chlorophytes, *C. closterium*, naviculoid cells) were frequently observed in natural water samples collected before the experiment. As the experiment progressed, other species appeared and some of them even became dominant e.g. *Pseudonitzchia* sp. H. Peragallo appeared after Julian day 197, *Leptocylindrus* sp. Cleve was observed after Julian day 204 while *Amphora* sp. Ehrenberg ex Kützing was notably present towards the end of the experiment (Fig. 5B). Other diatom species that were present throughout the experiment in a minor proportion were *Fragilaria* sp. Lyngbye and *Thalassiosira* sp. Cleve (data not shown). Dinoflagellates demonstrated a trend of increasing abundance of the large-sized (>20 µm) species such as *Prorocentrum mexicanum* Osorio-Tafall (Fig. 5D). On the other hand, flagellates were dominated by small chlorophytes (<10 µm) throughout the experiment, while larger chlorophytes (>10 µm) were also abundant and maintained steady growth throughout the experiment (Fig. 5E). Colorless flagellates increased their abundance from the initial time (Fig. 5F), while cryptophytes were present during most of the experiment but then declined towards the end of it (Fig. 5F).

3.3.3. Specific UVR and temperature effects

C. closterium, the most abundant diatom species, did not present any UVR effect but had a significantly lower contribution towards

Table 1
Daily growth rates (µ) based on biomass, for diatoms, autotrophic dinoflagellates, autotrophic flagellates and colorless plankton (heterotrophic dinoflagellates and flagellates) incubated at 28 °C and 31 °C. Radiation treatments are: PAB = PAR + UVR; P = PAR only. The values given are the means of duplicates with their half mean range.

Growth rate (µ; d^{-1})								
	Diatoms		Dinoflagellates		Flagellates		Colorless plankton	
	PAB	P	PAB	P	PAB	P	PAB	P
28 °C	0.47 ± 0.04	0.49 ± 0.04	0.24 ± 0.01	0.41 ± 0.07	0.16 ± 0.01	0.22 ± 0.04	0.22 ± 0.04	0.33 ± 0.03
31 °C	0.40 ± 0.01	0.43 ± 0.02	0.21 ± 0.06	0.31 ± 0.04	0.18 ± 0.05	0.20 ± 0.02	0.24 ± 0.03	0.19 ± 0.01

Table 2
Cell abundance-based growth rates (μ) for diatoms, autotrophic dinoflagellates, autotrophic flagellates and colorless plankton (heterotrophic dinoflagellates and flagellates) exposed to 28 °C and 31 °C. Radiation treatments are: PAB = PAR + UVR; P = PAR only. The values given are the means of duplicates with their half mean range.

Growth rate (μ; d^{-1})								
	Diatoms		Dinoflagellates		Flagellates		Colorless plankton	
	PAB	P	PAB	P	PAB	P	PAB	P
28 °C	0.43 ± 0.02	0.41 ± 0.04	0.23 ± 0.01	0.27 ± 0.05	0.24 ± 0.02	0.24 ± 0.01	0.20 ± 0.04	0.36 ± 0.04
31 °C	0.29 ± 0.02	0.36 ± 0.06	0.23 ± 0.03	0.28 ± 0.06	0.15 ± 0.02	0.23 ± 0.03	0.23 ± 0.01	0.21 ± 0.02

the end of the experiment to the total community abundance, at 31 °C than at 28 °C ($p < 0.05$; Fig. 6A, B). No significant differences in dominance were observed between ambient and increased temperatures in the other diatom species with the exception of *Pseudonitzchia* sp. that dominated only at Julian day 208 at 28 °C (Fig. 6A). UVR effects were observed in some of the diatom species such as *Leptocylindrus* sp. and *Amphora* sp. that were present in the P treatment but absent in the PAB treatment at 31 °C from Julian days 204 to 206 (Fig. 6B). Neither *Leptocylindrus* sp. nor *Amphora* sp. at 28 °C or other diatom species showed significant differences in their abundance among radiation treatments (Fig. 6A, B).

No interactive UVR-temperature effects were observed for any dinoflagellate species. During the first part of the experiment, small naked dinoflagellates species (<20 μm) dominated, together with other dinoflagellates (Fig. 7), but their contribution decreased as the experiment progressed. Following this decline, the armored dinoflagellate *P. mexicanum* increased its abundance, becoming one of the most frequent species towards the end of the experiment. Large naked dinoflagellates species (>20 μm) also increased their contribution, especially in the P treatment. There were no significant effects of UVR on *P. mexicanum*, at both temperatures; however, the large naked dinoflagellates had a major share in the UVR-excluded conditions ($p < 0.05$) at both temperatures. These large naked dinoflagellates also had a significantly higher contribution at increased temperature as compared to the control.

No interactive UVR-temperature effects were observed in flagellates with the exception of the large cryptophytes (>20 μm) that showed a synergistic effect in the interaction between UVR and temperature by disappearing in the PAB treatment at 31 °C (Fig. 8). Small cryptophytes (<10 μm) were present at 28 °C in a similar proportion in the PAB and P treatments during the first part of the experiment, but they decreased their contribution in the samples exposed to UVR (Fig. 8A). In the increased temperature microcosms (Fig. 8A), cryptophytes accounted for a significantly lower proportion than at 28 °C (Fig. 8B), while small chlorophytes decreased their contribution throughout the experiment at 28 °C, but maintained it towards the end under increased temperature conditions (Fig. 8A, B).

4. Discussion

Our research focused on assessing the combined effects of UVR and temperature on changes in community structure and growth of tropical plankton assemblages using microcosm experiments. Our approach was to maintain the cells within a limited water depth thus increasing the radiation (both PAR and UVR) relative to what they would normally receive in the water column if they were moving within the upper mixed layer (UML). The high levels of solar radiation received during our experiments are normally considered stressful for phytoplankton (Häder et al., 2011), although tropical species are acclimated to a history of high radiation levels (Banaszak and Lesser, 2009). Other studies simulated increased UVR with supplementary UVR sources (e.g., Rousseaux et al., 2004) but in our case we considered that using solar radiation and creating a "shallower UML" (i.e., cells within 15 cm of the water surface) clearly simulated an extreme condition of increased stratification due to climate change for this community. In this way, and when compared to the PAR control samples, we were able to estimate the influence of this enhanced UVR condition. In addition, we maintained an increased difference of 3 °C between temperature treatments, although some natural fluctuations occurred in both systems that are similar to those that occur within a shallow upper mixed layer (UML) (Behrenfeld et al., 2006). Thus the set of conditions imposed in our experiments can be considered a worst-case scenario for both the increase in solar UVR and temperature on these tropical communities.

Our study determined no significant interactions between UVR and temperature in the growth of any particular group, but changes in the size and structure within groups occurred along the experiment. This is in line with previous studies (Belzile et al., 2006) that showed that UVR will more likely affect the food web structure rather than bulk biomass due to the differential sensitivities between planktonic organisms. For instance, it has been argued that species living close to their temperature tolerance limit may be adversely influenced if temperature rises (Beardall and Raven, 2004). In our study two of the dominant species in the natural phytoplankton assemblage, the pennate diatoms *C. closterium* and *Pseudonitzchia* sp., were negatively affected by increased temperature, whereas UVR and temperature had synergistic negative effects on larger species such as *Leptocylindrus* sp. and *Amphora* sp. This impact on large cells at increased temperature resulted in a decrease in biomass of diatoms as observed in our study. Similarly, previous studies carried out with phytoplankton assemblages in mesocosms found a markedly lower phytoplankton biomass, especially of large-celled diatoms as a result of warming (Lewandowska

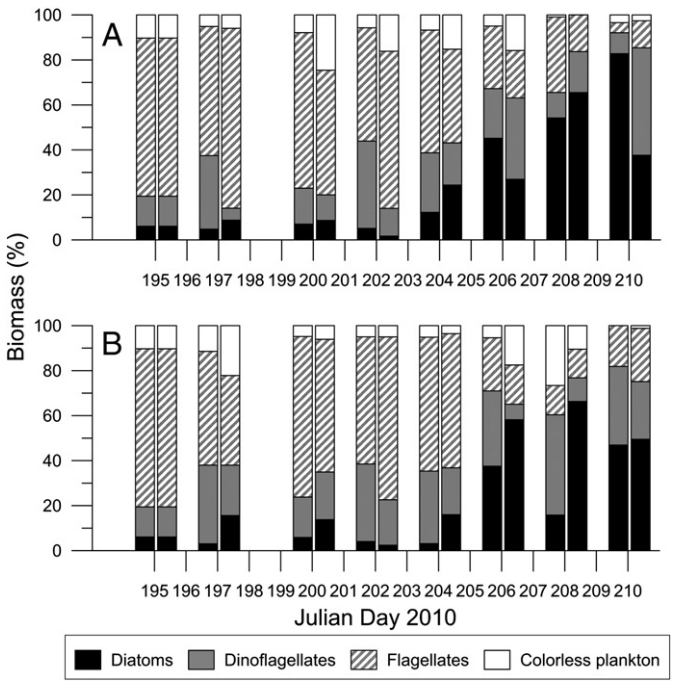

Fig. 3. Biomass contribution (in percentage) for diatoms, autotrophic dinoflagellates, autotrophic flagellates and colorless plankton (heterotrophic dinoflagellates and flagellates) in microcosms incubated at 28 °C (A) and 31 °C (B). Percentage values are the means of duplicates for each radiation treatment, which are shown beside each other: PAB on the left side and P on the right side of each pair.

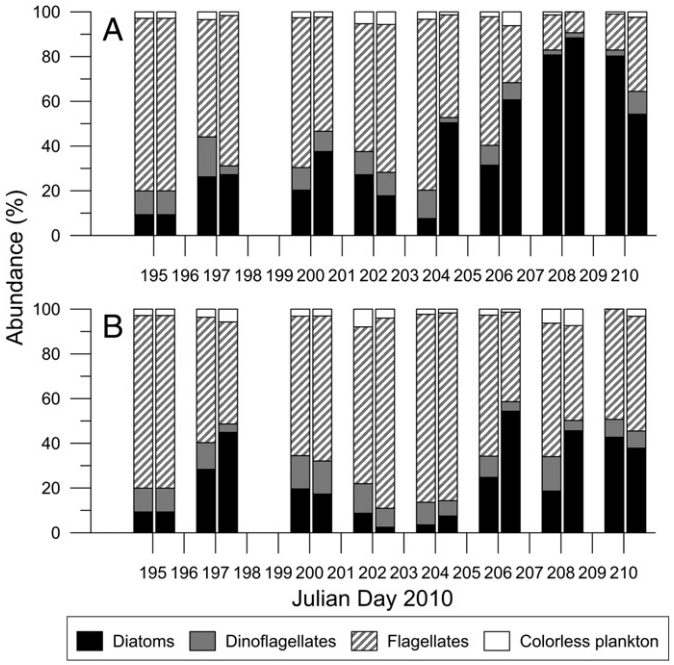

Fig. 4. Cell abundance contribution (in percentage) for diatoms, autotrophic dinoflagellates, autotrophic flagellates and colorless plankton (heterotrophic dinoflagellates and flagellates) in microcosms incubated at 28 °C (A) and 31 °C (B). Percentage values are the means of duplicates for each radiation treatment, which are shown beside each other: PAB on the left side and P on the right side of each pair.

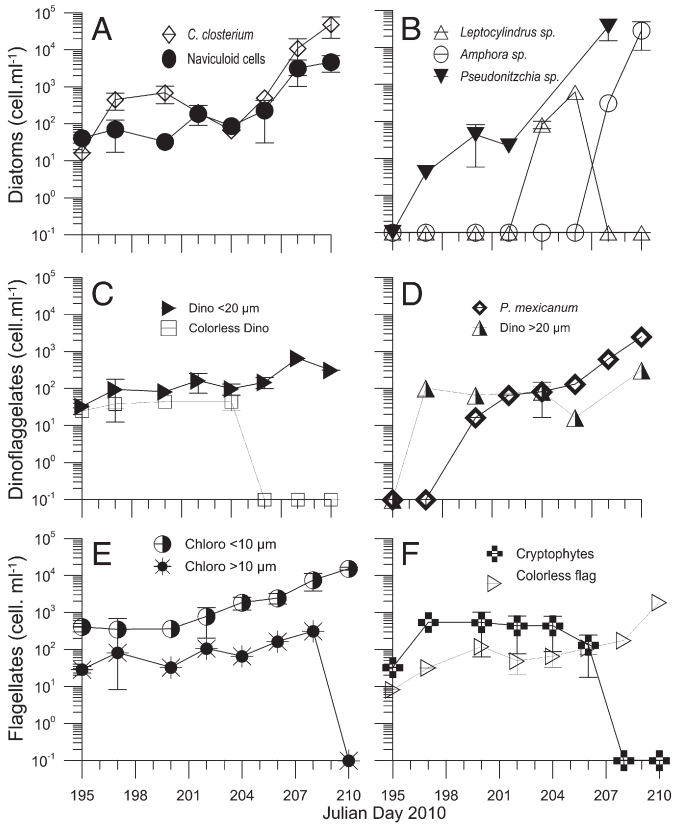

Fig. 5. Abundance succession (in cells ml^{-1}) of the more frequent species of diatoms (A, B) dinoflagellates (C, D) and flagellates (E, F) during the experiment (July 14th to 29th 2010) with seawater samples in the PAB treatment at 28 °C.

and Sommer, 2010; Wohlers et al., 2009). However, this negative response is not universal, as other studies carried out with natural marine phytoplankton assemblages showed that larger diatoms benefited by warming (Lionard et al., 2012; Thyssen et al., 2011). In our study, the changes in size were not only observed in diatoms but also in dinoflagellates that changed from small cells (i.e., <20 µm naked dinoflagellates) to bigger species (>20 µm; e.g., *P. mexicanum*). Some studies on the presence of UVR-absorbing compounds in microalgae have shown an especially high abundance among dinoflagellates including species of *Prorocentrum* Ehrenberg (Jeffrey et al., 1999; Llewellyn and Airs, 2010; Marcoval et al., 2007). Hence, the observed structural changes could be a consequence of the higher tolerance of large dinoflagellates species as compared to small cells. However, dinoflagellates had lower biomass in samples receiving UVR therefore this photoprotection strategy was probably not sufficient to cope with UVR. Similarly, Lesser (1996) observed inhibition of photosynthesis in cultured cells of *Prorocentrum micans* Ehrenberg despite the presence and accumulation of UVR-absorbing compounds. On the other hand, our results also showed that small chlorophytes were favored at increased temperature as compared to the control. In agreement with our results, previous studies have found a significant increase in the proportion of small-sized species (Daufresne et al., 2009; Winder et al., 2009), which is in accordance with the temperature-size rule. This rule states that individuals grown at cooler temperatures reach larger sizes than those reared at warmer temperatures (Forster et al., 2012). We cannot rule out, however, that part of the observed changes in size was related to nutrient conditions as large cells would benefit from the input of nutrients as in our experiment due to their relatively small surface-to-volume ratio as compared to smaller cells (Falkowski, 1981).

In general, it is assumed that temperature-regulated processes in cell metabolism (such as cell division, DNA repair, production of photoprotective pigments, and oxidative stress responses) may act faster than UVR-induced damage by accelerating biochemical processes (Baulch et al., 2005; Doyle et al., 2005). However, these conclusions are based on studies involving temperate phytoplankton communities, and therefore only consider lower temperatures. To our knowledge, no studies have been conducted on the combined effects of UVR and temperature on growth and composition of tropical phytoplankton communities, however, there are some studies that focus on the photosynthetic performance of tropical phytoplankton. For example, Banaszak et al. (2003) assessed the effects of thermal and light stress on the physiological status of dinoflagellate endosymbionts of corals and suggested that the cell thermal tolerance ranges could be exceeded as sea-surface temperatures increase because these symbionts live close to their maximal thermal tolerance range. Our results suggest that some diatom species could be thermally sensitive and would diminish their growth under increased sea-surface temperatures whereas small flagellate species would benefit. Therefore, this study highlights that the observed responses to the combination of UVR and temperature are species and size-specific and complex. Although diatoms are not major contributors in tropical communities, they could flourish under high nutrient conditions. So, it is important to consider the occurrence of diatom blooms in coastal areas exposed to nutrient enrichment due to anthropogenic activities. Our experiments simulated a scenario with an input of nutrients, and although no nutrient measurements were done along the experiment, the increase of the community biomass did not indicate any limitation. Hence, the responses observed here could be similar to those that would occur in a nutrient-enriched coastal area affected by increased UVR-temperature events. Although the study area is naturally oligotrophic, for example NH_4^+ concentrations range between 1.2 and 3.4 µM, DIN concentrations range from 2.8 to 5.1 µM and PO_4^{3-} concentrations range between 1.0 and 2.7 µM (Carruthers et al., 2005; Duarte et al., 1995), the concentrations of these nutrients can be augmented in coastal areas due to nutrient-laden freshwater entering from the ever-increasing impact of anthropogenic activities such as tourism-related development (Rodríguez-Martínez et al., 2010; van Tussenbroek, 2011). In accordance with our

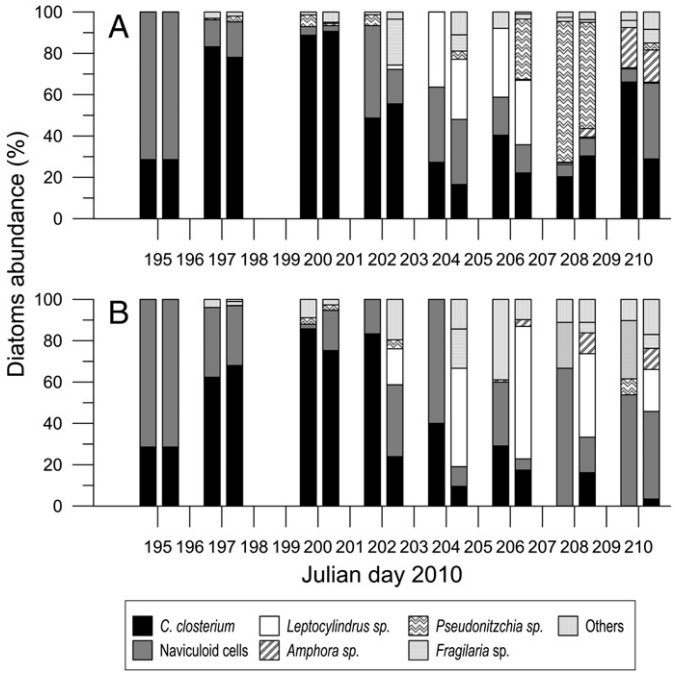

Fig. 6. Percentage contribution in terms of cell abundance for the more frequently found diatoms during the experiment (July 14th to 29th 2010) with seawater samples incubated at 28 °C (A) and 31 °C (B). Percentage values are the means of duplicates for each radiation treatment and were calculated based on the total abundance of diatoms. The different radiation treatments are shown beside each other: PAB on the left side and P on the right side of each pair.

results, the subsequent eutrophization of the coastal areas would favor diatoms. However, when coupled with higher sea-surface temperatures in combination with the high UVR levels, there would potentially be a counteracting effect on some diatom species.

Although there was no interactive effect of temperature and UVR on biomass accumulation, these two stressors did have a major impact on carbon biomass partitioning. Similar effects have been reported in several studies, which determined that changes in phytoplankton community structure caused by UVR can affect higher trophic levels (e.g., microzooplankton and copepod nauplii; Keller et al., 1997; Mostajir et al., 1999), as well as heterotrophic bacteria (Arrieta et al., 2000; Herndl et al., 1997). In this study we observed a decrease in the colorless plankton biomass (i.e., heterotrophic flagellates and dinoflagellates) due to UVR exposure that could probably be related to the direct negative effects of UVR, although indirect effects should not be disregarded. We did not take into account the potential interactive effects between plankton and heterotrophic bacteria, but they could be a source of food for heterotrophs. Hence, if heterotrophic bacteria were negatively affected by UVR (or temperature), indirect effects would occur on heterotrophic plankton. On the other hand, we consider that the impact of a potential nutrient release by bacteria would be minimal as compared to the full nutrient conditions in the microcosms. In relation to other indirect effects such as grazing, we considered it negligible, as we pre-screened our samples to remove large zooplankton. In addition, microscopic observations did not reveal any significant amounts of small zooplankton species.

Overall, the coupling of eutrophization with the studied factors could have important consequences on the structure of plankton communities, promoting the change in species composition of the whole plankton community. In line with this, Marcoval et al. (2008) found that natural phytoplankton samples exposed to solar radiation over a week showed different responses to different nutrient treatments with taxonomic changes being mostly due to nutrient availability, and to a lesser extent due to solar UVR exposure. In our study, plankton succession showed a similar pattern in all treatments, with a pronounced advantage of diatoms (probably due to nutrient addition), especially at the control temperature, where the dominant diatom species grew without thermal restrictions. In spite of the decreased contribution of the flagellate group to the whole community throughout the experiment, some small-sized species were favored by the increased temperature. In contrast, others were adversely affected by UVR. Hence, the full nutrient condition seems to have an important role in controlling the

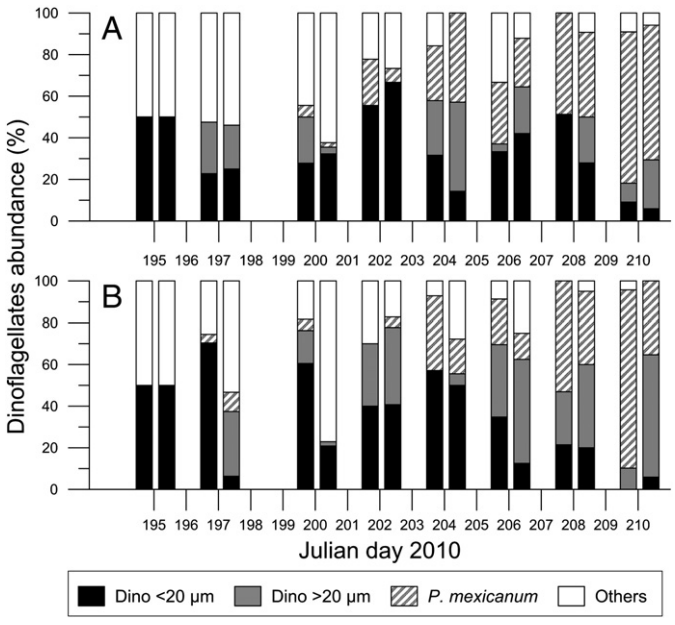

Fig. 7. Percentage contribution in terms of cell abundance for the more frequently found dinoflagellates during the experiment (July 14th to 29th 2010) with seawater samples incubated at 28 °C (A) and 31 °C (B). Percentage values are the means of duplicates for each radiation treatment and were calculated based on the total abundance of dinoflagellates. The different radiation treatments are shown beside each other: PAB on the left side and P on the right side of each pair.

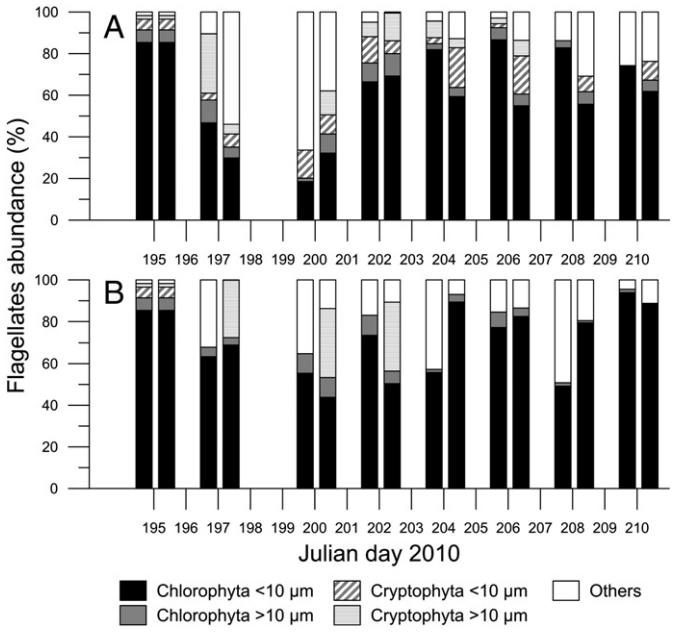

Fig. 8. Percentage contribution in terms of cell abundance for the more frequently found flagellates during the experiment (July 14th to 29th 2010) with seawater samples incubated at 28 °C (A) and 31 °C (B). Percentage values are the means of duplicates for each radiation treatment and were calculated based on the total abundance of flagellates. The different radiation treatments are shown beside each other: PAB on the left side and P on the right side of each pair.

trends in plankton succession while temperature and UVR shape the species composition.

In summary, our data highlight that although tropical plankton assemblages are generally well-adapted to high temperature and UVR fluxes, under prolonged and high radiation conditions, changes in community structure in terms of taxonomic composition and size distribution would occur. This would be a consequence of the specific impact of the studied factors: Some diatom species would be negatively affected by increased temperature, while small flagellates would be favored; UVR would mainly negatively affect naked dinoflagellates, cryptophyta and colorless flagellates. Further investigations are needed to assess the impact of these changes on tropical phytoplankton productivity as well as on other components of the trophic web.

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References

Arrieta, J., Weinbauer, M., Herndl, G., 2000. Interspecific variability in sensitivity to UV radiation and subsequent recovery in selected isolates of marine bacteria. Appl. Environ. Microbiol. 66, 1468–1473.

Banaszak, A.T., Lesser, M.P., 2009. Effects of solar ultraviolet radiation on coral reef organisms. Photochem. Photobiol. Sci. 8, 1276–1294.

Banaszak, A.T., Ayala-Schiaffino, B.N., Rodríguez-Román, A., Enríquez, S., Iglesias-Prieto, R., 2003. Response of *Millepora alcicornis* (Milleporina: Milleporidae) to two bleaching events at Puerto Morelos reef, Mexican Caribbean. Rev. Biol. Trop. 51, 57–66.

Baulch, H.M., Schindler, D.W., Turner, M.A., Findlay, D.L., Paterson, M.J., Vinebrooke, R.D., 2005. Effects of warming on benthic communities in a boreal lake: implications of climate change. Limnol. Oceanogr. 50, 1377–1392.

Beardall, J., Raven, J.A., 2004. The potential effects of global climate change on microalgal photosynthesis, growth and ecology. Phycologia 43, 26–40.

Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M., Boss, E.S., 2006. Climate-driven trends in contemporary ocean productivity. Nature 444, 752–755.

Belzile, C., Demers, S., Ferreyra, G., Schloss, I., Nozais, C., Lacoste, K., Mostajir, B., Roy, S., Gosselin, M., Pelletier, E., Gianesella, S., Vernet, M., 2006. UV effects on marine planktonic food webs: a synthesis of results from mesocosm studies. Photochem. Photobiol. 82, 850–856.

Buma, A.G.J., Visser, R.J.W., van de Poll, W.H., Villafañe, V.E., Janknegt, P.J., Helbling, E.W., 2009. Wavelength dependent xanthophyll cycle activity in marine microalgae exposed to natural ultraviolet radiation. Eur. J. Phycol. 44, 515–524.

Carruthers, T.J.B., van Tussenbroek, B.I., Dennison, W.C., 2005. Influence of submarine springs and wastewater on nutrient dynamics of Caribbean seagrass meadows. Estuar. Coast. Shelf Sci. 64, 191–199.

Daufresne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic ecosystems. Proc. Natl. Acad. Sci. U. S. A. 106, 12788–12793.

Davison, I.R., 1991. Environmental effects on algal photosynthesis: temperature. J. Phycol. 27, 2–8.

Diaz, H.F., Graham, N.E., 1996. Recent changes in tropical freezing heights and the role of sea surface temperature. Nature 383, 152–155.

Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., 2008. Ocean acidification: the other CO_2 problem. Annu. Rev. Mater. Sci. 1, 169–192.

Doyle, S., Saros, J.E., Williamson, C.E., 2005. Interactive effects of temperature and nutrient limitation on the response of alpine phytoplankton growth to UV radiation. Limnol. Oceanogr. 50, 1362–1367.

Duarte, C.M., Merino, M., Gallegos, M., 1995. Evidence of iron deficiency in seagrasses growing above carbonate sediments. Limnol. Oceanogr. 40, 1153–1158.

Falkowski, P.G., 1981. Light shade adaptation and assimilation numbers. J. Plankton Res. 3, 203–216.

Forster, J., Hirst, A.G., Esteban, G.F., 2012. Achieving temperature-size changes in a unicellular organism. ISME J. 7, 28–36.

Guillard, R.R.L., Ryther, J.H., 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt and *Detonula confervacea* (Cleve) Gran. Can. J. Microbiol. 8, 229–239.

Häder, D.-P., Helbling, E.W., Williamson, C.E., Worrest, R.C., 2011. Effects of UV radiation on aquatic ecosystems and interactions with climate change. Photochem. Photobiol. Sci. 10, 242–260.

Halac, S.R., Villafañe, V.E., Helbling, E.W., 2010. Temperature benefits the photosynthetic performance of the diatoms *Chaetoceros gracilis* and *Thalassiosira weissflogii* when exposed to UVR. J. Photochem. Photobiol. B Biol. 101, 196–205.

Helbling, E.W., Villafañe, V.E., Ferrario, M., Holm-Hansen, O., 1992. Impact of natural ultraviolet radiation on rates of photosynthesis and on specific marine phytoplankton species. Mar. Ecol. Prog. Ser. 80, 89–100.

Herndl, G., Brugger, A., Hager, S., Kaiser, E., Obernosterer, I., Reitner, B., Slezak, D., 1997. Role of ultraviolet-B radiation on bacterioplankton and the availability of dissolved organic matter. Vegetatio 128, 43–51.

Hillebrand, H., Dürselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 403–424.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A., 2001. Climate Change 2001. Cambridge Univ. Press, New York.

IPCC, 2007. Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.Cambridge Univ. Press, New York.

Jeffrey, S.W., Mactavish, H.S., Dunlap, W.C., Vesk, M., Groenewoud, K., 1999. Occurrence of UVA and UVB-absorbing compounds in 152 species (306 strains) of marine microalgae. Mar. Ecol. Prog. Ser. 189, 35–51.

Johnson, N.C., Xie, S.P., 2010. Changes in the sea surface temperature threshold for tropical convection. Nat. Geosci. 3, 842–845.

Keller, A., Hargraves, P., Jeon, H., Klein-Macphee, G., Klos, E., Oviatt, C., Zhang, J., 1997. Effects of ultraviolet-B enhancement on marine trophic levels in a stratified coastal system. Mar. Biol. 130, 277–287.

Lassen, M.K., Nielsen, K.D., Richardson, K., Garde, K., Schlüter, L., 2010. The effects of temperature increases on a temperate phytoplankton community — a mesocosm climate change scenario. J. Exp. Mar. Biol. Ecol. 383, 79–88.

LeGresley, C.M., McDermott, G., 2010. Counting chamber methods for quantitative phytoplankton analysis — haemocytometer, Palmer-Maloney cell and Sedgewick-Rafter cell. In: Karlson, B., Cusack, C., Bresnan, E. (Eds.), Microscopic and Molecular Methods for Quantitative Phytoplankton Analysis Intergovernmental Oceanographic Commission (IOC), Manuals and Guides, UNESCO, pp. 25–30.

Lesser, M.P., 1996. Acclimation of phytoplankton to UV-B radiation: oxidative stress and photoinhibition of photosynthesis are not prevented by UV-absorbing compounds in the dinoflagellate *Prorocentrum micans*. Mar. Ecol. Prog. Ser. 132, 287–297.

Levitus, S., Antonov, J.I., Boyer, T.P., Stephens, C., 2000. Warming of the world ocean. Science 287, 2225–2229.

Lewandowska, A., Sommer, U., 2010. Climate change and the spring bloom: a mesocosm study on the influence of light and temperature on phytoplankton and mesozooplankton. Mar. Ecol. Prog. Ser. 405, 101–111.

Lionard, M., Roy, S., Tremblay-Létourneau, M., Ferreyra, G.A., 2012. Combined effects of increased UV-B and temperature on the pigment-determined marine phytoplankton community of the St. Lawrence Estuary. Mar. Ecol. Prog. Ser. 445, 219–234.

Llewellyn, C.A., Airs, R.L., 2010. Distribution and abundance of MAAs in 33 species of microalgae across 13 classes. Mar. Drugs 8, 1273–1291.

MacFadyen, E.J., Williamson, C.E., Grad, G., Lowery, M., Jeffrey, W.H., Mitchell, D.L., 2004. Molecular response to climate change: temperature dependence of UVR-induced DNA damage and repair in the freshwater crustacean *Daphnia pulicaria*. Glob. Change Biol. 10, 408–416.

Madronich, S., 1993. The atmosphere and UV-B radiation at ground level. In: Young, A.R., Björn, L.O., Moan, J., Nultsch, W. (Eds.), Environmental UV Photobiology. Plenum Press, New York, pp. 1–39.

Marcoval, M.A., Villafañe, V.E., Helbling, E.W., 2007. Interactive effects of ultraviolet radiation and nutrient addition on growth and photosynthesis performance of four species of marine phytoplankton. J. Photochem. Photobiol. B Biol. 89, 78–87.

Marcoval, M.A., Villafañe, V.E., Helbling, E.W., 2008. Combined effects of solar ultraviolet radiation and nutrients addition on growth, biomass and taxonomic composition of coastal marine phytoplankton communities of Patagonia. J. Photochem. Photobiol. B Biol. 91, 157–166.

Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and of the protist plankton. Limnol. Oceanogr. 45, 569–579.

Mostajir, B., Demers, S., de Mora, S., Belzile, C., Chanut, J.-P., Gosselin, M., Roy, S., Villegas, P.Z., Fauchot, J., Bouchard, J.N., Bird, D., Monfort, P., Levasseur, M., 1999. Experimental test of the effect of ultraviolet-B radiation in a planktonic community. Limnol. Oceanogr. 44, 586–596.

Nilawati, J., Greenberg, B.M., Smith, R.E.H., 1997. Influence of ultraviolet radiation on growth and photosynthesis of two cold ocean diatoms. J. Phycol. 33, 215–224.

Rae, R., Vincent, W.F., 1998. Effects of temperature and ultraviolet radiation on microbial food web structure: potential response to global change. Freshw. Biol. 40, 747–758.

Rodríguez-Martínez, R.E., Ruíz-Rentería, F., van Tussenbroek, B., Barba-Santos, M.G., Escalante-Mancera, E., Jordán-Garza, G., Jordán-Dahlgren, E., 2010. State and environmental tendencies of the Puerto Morelos CARICOMP site, Mexico. Rev. Biol. Trop. 58, 23–43.

Roemmich, D., Gilson, J., 2009. The 2004–2008 mean and annual cycle of temperature, salinity, and steric height in the global ocean from Argo Program. Prog. Oceanogr. 82, 81–100.

Rousseaux, M.C., Flint, S.D., Searles, P.S., Caldwell, M.M., 2004. Plant responses to current solar ultraviolet-B radiation and to supplemented solar ultraviolet-B radiation simulating ozone depletion: an experimental comparison. Photochem. Photobiol. 80, 224–230.

Roy, S., Mohovic, B., Gianesella, S.M.F., Schloss, I.R., Ferrario, M.E., Demers, S., 2006. Effects of enhanced UV-B on pigment-based phytoplankton biomass and composition of mesocosm-enclosed natural marine communities from three latitudes. Photochem. Photobiol. 82, 909–922.
Ruggaber, A., Dlugi, R., Nakajima, T., 1994. Modelling of radiation quantities and photolysis frequencies in the troposphere. J. Atmos. Chem. 18, 171–210.
Sobrino, C., Neale, P.J., 2007. Short-term and long-term effects of temperature on photosynthesis in the diatom *Thalassiosira pseudonana* under UVR exposures. J. Phycol. 43, 426–436.
Staehelin, J., Harris, N.R.P., Appenzeller, C., Ebenhard, J., 2001. Ozone trends: a review. Rev. Geophys. 39, 231–290.
Stott, P.A., Kettleborough, J.A., 2002. Origins and estimates of uncertainty in predictions of twenty-first century temperature rise. Nature 416, 723–726.
Thyssen, M., Ferreyra, G., Moreau, S., Schloss, I., Denis, M., Demers, S., 2011. The combined effect of ultraviolet B radiation and temperature increase on phytoplankton dynamics and cell cycle using pulse shape recording flow cytometry. J. Exp. Mar. Biol. Ecol. 406, 95–107.
Tomas, C.R., 1997. Identifying Marine Phytoplankton. Academic Press, San Diego (858 pp.).
van Tussenbroek, B.I., 2011. Dynamics of seagrasses and associated algae in coral reef lagoons. Hidrobiológica 21, 293–310.
Villafañe, V.E., Reid, F.M.H., 1995. Métodos de microscopía para la cuantificación del fitoplancton. In: Alveal, K., Ferrario, M.E., Oliveira, E.C., Sar, E. (Eds.), Manual de Métodos Ficológicos. Universidad de Concepción, Concepción, Chile, pp. 169–185.
Wängberg, S.Å., Garde, K., Gustavson, K., Selmer, J.S., 1999. Effects of UVB radiation on marine phytoplankton communities. J. Plankton Res. 21, 147–166.
Whitehead, R.F., de Mora, S., Demers, S., Gosselin, M., Monfort, P., Mostajir, B., 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.
Williamson, C.E., Grad, G., Gilroy, S., De Lange, H.J., Karapelou, D.M., 2002. Temperature dependent UV responses in zooplankton: implications of climate change. Limnol. Oceanogr. 47, 1844–1848.
Winder, M., Reuter, J.E., Schladow, S.G., 2009. Lake warming favours small-sized planktonic diatom species. Proc. R. Soc. B 276, 427–435.
Wohlers, J., Engel, A., Zöllner, E., Breithaupt, P., Jürgens, K., Hoppe, H., Sommer, U., Riebesell, U., 2009. Changes in biogenic carbon flow in response to sea surface warming. Proc. Natl. Acad. Sci. U. S. A. 106, 7067–7072.
Xenopoulos, M.A., Leavitt, P.R., Schindler, D.W., 2009. Ecosystem— level regulation of boreal lake phytoplankton by ultraviolet radiation. Can. J. Fish. Aquat. Sci. 66, 2002–2010.
Zar, J.H., 1984. Biostatistical Analysis. Prentice Hall, Englewood Cliffs, NJ.