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Microbial carbon and nitrogen production under experimental conditions combining warming with increased ultraviolet-B radiation in Mediterranean coastal waters

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ABSTRACT

The effects of warming and increased ultraviolet-B radiation (UVBR, 280–320 nm) have been rarely studied at food web scale and very few studies have considered the effect of combining these two climatic stressors. Microbial carbon and nitrogen dynamics were studied under the single and combined conditions of +3 °C warming and +20% UVBR above the natural levels (control) during a 10-day mesocosm experiment in coastal Mediterranean waters. The effect of increased UVBR on primary production (PP) and bacterial production (BP) rates was rarely significant during the experiment. Warming alone or combined with increased UVBR significantly reduced BP by about 30% but also significantly increased PP by an average of 90%. No accumulation of particulate organic matter was observed during the experiment but, in the warmed mesocosms, the cumulative carbon and nitrogen losses were greater (ca. +40%). The main short-term consequence of warming was, therefore, a shift of the food web dynamics leading to higher C and N losses. This suggests a more efficient transfer of the newly produced microbial production to the upper trophic levels and a greater exportation into deeper waters through settlement under warmer conditions in Mediterranean coastal waters in the future.

1. Introduction

Given their global importance as ecosystem goods and services, coastal marine environments are of major concern in terms of the potential impact of anthropogenic climate change. Mediterranean coastal waters are considered to be a hotspot of species diversity and to be particularly affected by climate change (Blue Plan Report, 2001; Lejeusne et al., 2010). Since 1979, there has been an increase in UVBR in the northern hemisphere mid-latitude of 7% during winter/spring and of 4% in summer/autumn (data from UNEP, 1999). The penetration of short wavelength solar radiation in water depends strongly on the content of dissolved and particulate substances as well as on the concentration of phytoplankton biomass. A comparison of the vertical distribution of phytoplankton and UVBR penetration indicated that the primary producers in the coastal waters of the Mediterranean, characterized by low concentrations of chromophoric dissolved organic matter (cDOM) and sestonic material, are affected by short wavelength solar radiation (Häder, 1997). Picophytoplankton from Mediterranean coastal waters showed differences in sensitivity to solar ultraviolet radiation (Sommaruga et al., 2005) and the net community production and bacterial metabolism from north-western Mediterranean waters were affected by ultraviolet radiation penetration (Joux et al., 2009). Previous studies on the effect of increased UVBR alone on the microbial communities in various geographical areas showed that the community response and associated N and C dynamics depended strongly on the nutrient status, pre-acclimation, mixing regime and community composition (reviewed by Belzile et al., 2006). Furthermore, increased UVBR usually had a greater direct effect on grazers than on autotrophic communities (Belzile et al., 2006). This may indirectly affect trophic interactions and nutrient availability. Although increased UVBR has been reported to reduce C and N uptake rates in the short term (Döhler, 1992; Döhler ,1997; Behrenfeld et al., 1995; Fauchot et al., 2000; Mousseau et al., 2000; Fouilland et al., 2003), repair mechanisms may reduce the harmful consequences of increased UVBR in the longer term (Belzile et al., 2006).

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Increased UVBR is not the only consequence of global climate change. The Mediterranean Sea has undergone profound physical changes over recent decades including increases in temperature (Béthoux et al., 1990; The MerMex Group, 2011). Over the last 30 years there has been an increase in the deep-water temperature, initially reported as a possible result of global warming (Béthoux et al., 1990). Increasing the seawater temperature increases heterotrophic bacterial processes (Sarmento et al., 2010). This suggests that warming may increase the C and N production through bacterial recycling processes and, therefore, may have a positive effect on the microbial food web. However, top-down factors may have a greater control on bacteria dynamics than any potential direct effect of simulated climate change (Bouvy et al., 2011). This was highlighted during a 10 day mesocosm experiment conducted in April 2006 showing that warming affected trophic interactions within the spring Mediterranean plankton community to a greater extent than increases in UVBR (Vidussi et al., 2011). The authors found that a significant reduction of heterotrophic bacteria biomass was the main consequence of warming with no apparent significant consequence on autotrophic biomass. The only consequence of the trophic-cascade effect under warming may have been a reduction in heterotrophic bacteria production rates. Warming may have encouraged autotrophic production leading to a more efficient transfer to the higher trophic levels. This hypothesis was tested during the same experiment. This article describes the effect on microbial C and N production rates of increasing UVBR and temperature, separately and in combination. The carbon and nitrogen uptake rates for phytoplankton and bacteria were compared to the dynamics of the organic matter measured under the various experimental conditions.

2. Material and methods

2.1. Experimental protocol

The mesocosm experiment was conducted from March 29 to April 7, 2006 in a coastal lagoon in the north-western Mediterranean (Thau lagoon, South of France: 43°24′N, 3°41′E). The experiment used the MEDIMEER (Mediterranean Center for Marine Ecosystem Experimental Research) facilities and instrumentation located on the shore of the Thau Lagoon. The experimental design was described in detail by Nouguier et al. (2007) and Vidussi et al. (2011). Eight moored mesocosms made of vinyl acetate/polyethylene bags (1.2 m diameter, 2 m depth, volume 2260 L) transmitting 77% and 53% of incident PAR and UVBR, respectively, were filled simultaneously at the same flow rates on March 29 (day 1) with screened (1000 μm) pooled lagoon surface water adjacent to the MEDIMEER pontoon. Duplicate mesocosms were subjected to i) a 20% increase in UVBR (UV), ii) a 3 °C increase in temperature (T) and iii) a 20% increase in UVBR with a 3 °C increase in temperature (UVT) and compared to duplicate control mesocosms with natural UVBR and temperature (CONT). The water temperature was monitored continuously (Campbell Scientific 107-L thermistor probes) at 3 different depths (0.5 m, 1 m and 1.5 m) in each mesocosm. The temperature in the CONT mesocosms was used as a reference and the temperature in the T and UVT mesocosms was continuously adjusted automatically, using heating elements (Galvatec, France) to maintain a positive difference of 3 °C from day 2 until the end of the experiment (Nouguier et al., 2007).

The incident solar spectrum from UVBR to near infrared radiation was recorded continuously using two RAMSES spectroradiometers (TriOS). The incident UVBR reference was continuously measured using a UV sensor (SKU 430, Skye Instruments). The UVBR in the UV and UVT mesocosms was maintained 20% higher than the incident light using UVB fluorescent lamps (Philips, TL20RS/01) that were adjusted automatically. The UV lamps were switched on every day from 08.45 to 16.45 UT from day 3 to the end of the experiment.

The water in each mesocosm was homogenized by pumping water continuously from 40 cm below the mesocosm surface water and releasing it at 40 cm above the bottom of the mesocosm to ensure recirculation of the whole mesocosm volume every hour. The eight mesocosms were usually sampled at about 08.30 UT every morning. Samples were collected immediately after filling up the mesocosms on March 29 to measure the initial nitrate and phosphate concentrations, as well as the bacterial abundance and chlorophyll *a* concentration. From day 2 onwards, all the variables presented in the paper were recorded daily (see below) at about 08.30 UT every morning.

2. 2. Concentrations of dissolved inorganic and organic nutrients

Ammonium concentrations were measured, immediately after the water had been collected, in unfiltered samples (50 mL, in triplicates) using a spectrophotometer (Hitachi U-3000) and the indophenol blue method (Koroleff, 1983). For nitrate (NO_3) and phosphate (PO_4) analysis, 80 mL of water was filtered through pre-combusted (450 °C, 5 h) glass-fiber filters (Whatman GF/F, 47 mm) and then stored frozen (−20 °C) until analysis using an automated colorimeter (Skalar) according to standard nutrient analysis methods (Tréguer and Le Corre, 1975).

For dissolved organic carbon (DOC) analysis, 10 mL of water was filtered through pre-combusted glass-fiber filters (Whatman GF/F, 47 mm). 10 μL of H_3PO_4 (85%) was added before storage at room temperature. The DOC concentrations were analyzed using a Shimadzu TOC-5000 Total Carbon Analyzer with a quartz combustion column filled with 1.2% Pt on silica pillows. Several features of this modified unit have already been described (Sohrin and Sempéré, 2005).

2.3. Concentrations of particulate organic nitrogen and carbon, microbial uptake rates of dissolved inorganic nitrogen and primary carbon production

The nitrogen and carbon uptake rates (microbial N uptake rates and primary production (PP), respectively) were estimated using the tracer method described by Dugdale and Wilkerson (1986). Traces of ^{15}N and ^{13}C isotopes ($Na^{15}NO_3$, $(^{15}NH_4)_2SO_4$ and $NaH^{13}CO_3^-$) were added to 500 mL subsamples, to give a final concentration of 0.05 $\mu mol\ L^{-1}$ for $^{15}NO_3^-$ and $^{15}NH_4^+$, 100 $\mu mol\ L^{-1}$ for $NaH^{13}CO_3^-$. The inoculated subsamples were incubated in Whirlpak polyethylene bags. The bags were immersed in the center of their corresponding mesocosms at the surface for 4 h (from 10:00 to 14:00 UT). The subsamples were then filtered onto precombusted Whatman GF/F filters and the filters were stored frozen at −80 °C. The samples were pelletized after being dried at 60 °C for 24 h and analyzed for ^{15}N and ^{13}C particulate organic nitrogen (PON) and carbon (POC) using a Europa Scientific ANCA mass spectrometer. Nitrogen and carbon uptake rates were calculated using the following Eq. (1) in Dugdale and Wilkerson (1986):

$$\rho = \frac{[C_p - C_0]}{[C_d - C_0] \times \Delta t} \times \frac{POM_f}{Vol} \rho \qquad (1)$$

where C_p is the concentration of the labeled compound (in atom %) in the particulate phase after incubation, C_d is the concentration of the labeled compound (in atom %) in the dissolved phase at time zero, C_0 is the natural concentration of the labeled compound (in atom %), i.e. 0.366% for ^{15}N and 1.11% for ^{13}C, Δt is the incubation time, POM_f is the particulate organic matter (carbon or nitrogen) at the end of the incubation and Vol is the filtered volume. The total dissolved inorganic carbon was estimated from salinity measurements as described by Strickland and Parsons (1968). The values of the ammonium uptake rates were corrected for the isotope dilution effect (Kanda et al., 1987) assuming that the regeneration rates and uptake rates were equivalent.

This assumption was confirmed by the net daily change of ammonium concentrations converted into hourly rates when compared to the uptake rates measured during the experiment.

2.4. Bacterial carbon production

Bacterial production (BP) was measured using ^{3}H-thymidine, using a protocol derived from Smith and Azam (1992). Duplicate 1.5 mL subsamples from each mesocosm were incubated with 20 nmol L^{-1} (final concentration) ^{3}H-[methyl]thymidine (Perkin Elmer, 1.5 TBq $mmol^{-1}$) in 2 mL microcentrifuge tubes. After 1 hour incubation in the dark at in situ temperature, 70 µL of 100% of trichloroacetic acid (TCA, 5% final concentration) was added to the microcentrifuge tubes and the macromolecules were allowed to precipitate for 15 min at 4 °C. Controls were performed by adding 100% TCA before the labeled thymidine. The tubes were then centrifuged for 10 min at 13,000 rpm (4 °C). The supernatant was discarded and the pellet was resuspended with 1.5 mL 5% TCA. This step was repeated 3 times and 1.5 mL of scintillation cocktail (Ultima Gold MV, Perkin Elmer) was then added to the final pellet. The radioactivity in the sample was determined using a liquid scintillation counter (Beckman LS 6500) and quench correction was made using external standards. BP was assessed using 2×10^{18} cells mol^{-1} TdR (Bell, 1990) and assuming 20 fgC $cell^{-1}$ (Lee and Fuhrman, 1987).

2.5. Estimation of cumulative microbial carbon and nitrogen losses

The carbon and nitrogen losses were estimated from daily measurements of microbial C and N production rates, considered as net C and N production, and from the daily variations in POC and PON concentrations (i.e. net POC and PON build up) using the following Eq. (2):

$$C(or\ N)losses = \text{Net C(or N)Production}-\text{POC(orPON)Change}. \qquad (2)$$

For each sampling day, the Net C daily production was the sum of the BP and PP rates converted into µmol CL^{-1} using the hourly rates multiplied by 13 h corresponding to the light period for PP and by 24 h for BP.

For each sampling day, the Net N daily production was the sum of NH_4 and NO_3 uptake rates converted into µmol N L^{-1} day^{-1}, assuming that bacteria can take up ca. 50% of the total N uptake rates as measured in these waters by Trottet et al. (2011) and using the hourly rates multiplied by 13 h of light for the phytoplanktonic uptake and 24 h for the bacterial uptake.

For each sampling day, the daily changes in POC and PON were calculated as the difference in the concentrations of POC and PON between two consecutive days and expressed in µmol L^{-1}.

The C and N losses calculated for each sampling day using Eq. (2) were then summed over the experiment period (until day 9).

2.5. Statistical analyses

One-way analyses of variance for repeated measurements (RM-ANOVA, Systat v.11) were performed on the chemical and biological variables to test the significance of the effects of single and combined UVBR and temperature treatments relative to the control. The values were within the same order of magnitude and were generally distributed normally as confirmed by using a normal probability plot and the one-sample Kolmogorov–Smirnov test. The ANOVA sphericity assumption was tested using Huynh–Feldt's estimate for epsilon (Scheiner and Gurevitch, 1993). ANOVA was then used to test the difference between the modified conditions (UV, T, UVT) and the controls (CONT) for each sampling day (Zar, 1984). The ANOVA was followed by an a posteriori contrast test, Fisher's LSD test (least significant difference; Zar, 1984). The significance threshold was set at $p \leq 0.05$.

3. Results

3.1. Water temperature and UVBR experimental conditions

The water temperature in the mesocosms increased by 2 °C over the first 6 days of the experiment. A difference of 3 °C was successfully maintained between non-heated and heated mesocosms throughout the whole experiment (Fig. 1A). No difference was detected between the non-heated mesocosms or between the heated mesocosms. The cumulative natural incident UVBR dose reached 349 kJ m^{-2} in CONT and was 20% greater (420 kJ m^{-2}) in the mesocosms with artificially increased UVBR (Fig. 1B).

3.2. Concentrations of dissolved inorganic and organic matter

Ammonium concentrations varied between 0.05 and 0.67 µmol L^{-1} in all the mesocosms with the lowest values mainly observed during the last period of the experiment. There were occasional significant differences between the UV, T and UVT mesocosms and the controls (ANOVA, $p \leq 0.05$) but without any consistent pattern. Nitrate concentrations decreased significantly from 1.1 to 0.05 µmol L^{-1} throughout

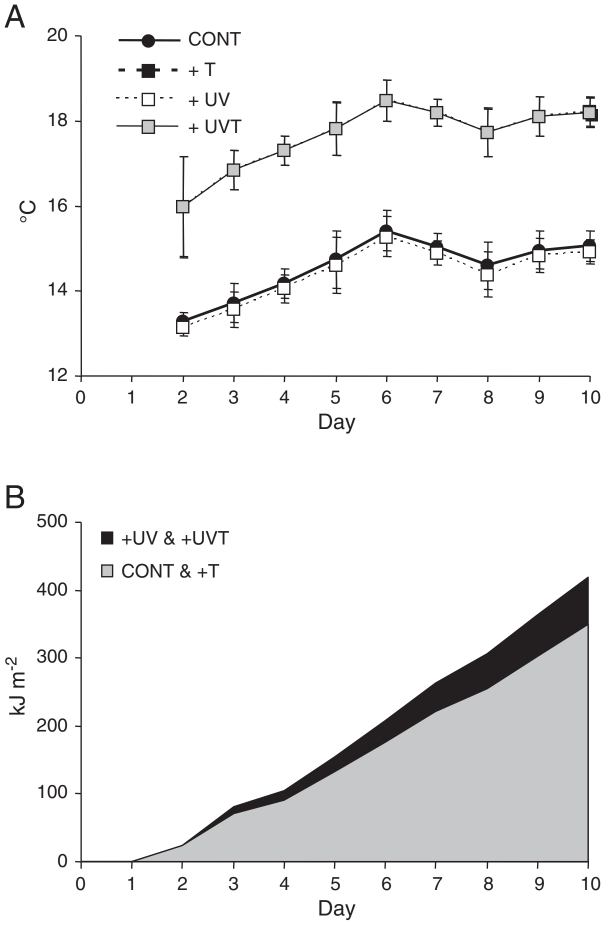

Fig. 1. (A) The water temperature in the mesocosms at 3 °C warming (T) over the natural temperature, a 20% increase in UVBR (UV) relative to the natural ambient level, a combined 3 °C increase in temperature and 20% increase in UVBR (UVT) and at natural UVBR and water temperature (CONT). Averages and standard deviations were calculated from measurements taken every 10 min at three depths in each mesocosm. (B) The cumulative dose of natural UVBR (received at the water surface of CONT and T mesocosms) and artificial UVBR dose in addition to the natural UVBR (received at the water surface of UV and UVT mesocosms).

the experiment in all the mesocosms but there were no significant differences between the UV, T and UVT mesocosms and the controls. Low phosphate concentrations (less than 0.06 µmol L^{-1}) increased in all the mesocosms until day 8, reaching a maximum of 0.1 µmol L^{-1}, and decreased thereafter. Some significant effects of increased temperature and UVBR were found on the last 2 days of the experiment (ANOVA, $p \leq 0.05$) but without any consistent pattern. Concentrations of DOC varied between 204 and 579 µmol L^{-1} in all the mesocosms during the experiment and there were no significant differences between the UV, T and UVT mesocosms and the controls except on day 4 (ANOVA, $p \leq 0.05$).

3.3. Concentrations of particulate organic carbon and nitrogen

Concentrations of particulate organic carbon (POC) increased slightly in all the mesocosms from 26 µmol L^{-1} to 32 µmol L^{-1} on average (Fig. 2A). UV had significantly lower POC concentrations throughout the experiment (RM-ANOVA, $p = 0.02$), whereas T and UVT only had significantly reduced POC concentrations on certain days (ANOVA, $p \leq 0.05$) (days 3, 5, 6 and 10).

Concentrations of particulate organic nitrogen (PON) varied between 1 and 5 µmol L^{-1} in all the mesocosms (Fig. 2B). There were no significant differences between UV or T mesocosms and the controls. However, the UVT mesocosm had generally lower PON concentration throughout the experiment (RM-ANOVA, $p = 0.05$), which was significant on days 6 and 10 (ANOVA, $p \leq 0.05$).

3.4. Dissolved inorganic nitrogen uptake rates

The absolute ammonium uptake rates decreased from day 2 to day 6 in all the mesocosms (from 67 to 9 nmol N L^{-1} h^{-1}, Fig. 3A) and increased afterwards. However, there was no significant difference between any of the UV, T and UVT mesocosms and the controls.

The absolute nitrate uptake rates increased in all the mesocosms from an average of 9 nmol N L^{-1} h^{-1} to an average of 21 nmol N L^{-1} h^{-1} (Fig. 3B). There was no significant difference between UV or UVT and the controls but the nitrate uptake rate was significantly higher in the T mesocosm (ANOVA, $p \leq 0.05$) on one occasion only (Fig. 3B).

3.5. Primary and bacterial C production

Primary production (PP) was estimated from the dissolved inorganic ^{13}C-NaHCO$_3$ uptake rates. PP increased throughout the experiment and reached significantly higher rates (ANOVA, $p \leq 0.05$) in the T and UVT mesocosms than in the controls (Fig. 4A). There was no significant difference between the UV mesocosms and the controls.

Bacterial production (PB) increased in the controls from day 2 (110 nmol CL^{-1} h^{-1}) to day 4 (240 nmol CL^{-1} h^{-1}) and decreased thereafter to reach the lowest values (average of 80 nmol CL^{-1} h^{-1}) on days 7, 8 and 9. There was a significant reduction in BP (ANOVA, $p \leq 0.05$) in the UV mesocosms (on day 6) and in the T and UVT mesocosms (on days 4, 5 and 6, Fig. 4B).

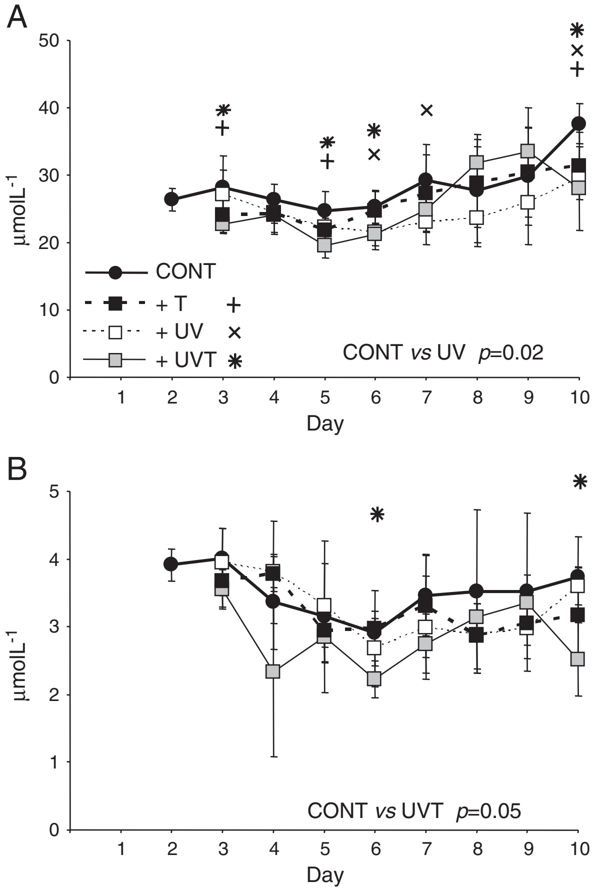

Fig. 2. Concentrations of (A) particulate organic carbon (POC), and (B) particulate organic nitrogen (PON) in the mesocosms in the three experimental conditions and in the control (see Fig. 1 for details). Crosses and asterisks denote significant differences between the UV, T and UVT mesocosms and the controls (CONT). RM-ANOVA results are provided when differences were statistically significant ($p \leq 0.05$).

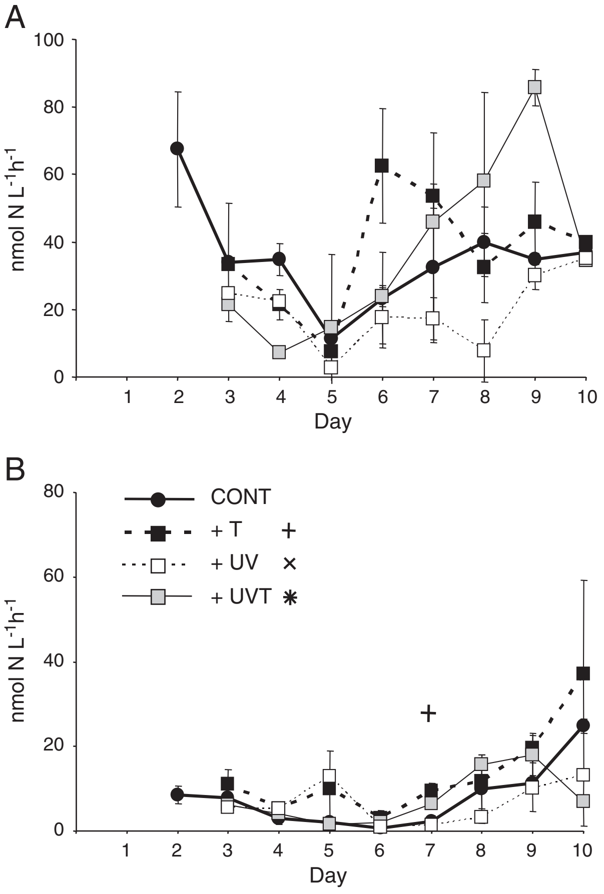

Fig. 3. Ammonium and nitrate (A and B) absolute uptake rates (ρN) in the UV, T and UVT mesocosms and the controls (CONT) (see Fig. 1 for details). Crosses and asterisks denote significant differences between the UV, T and UVT mesocosms and the controls (CONT) RM-ANOVA results are provided when differences were statistically significant ($p \leq 0.05$).

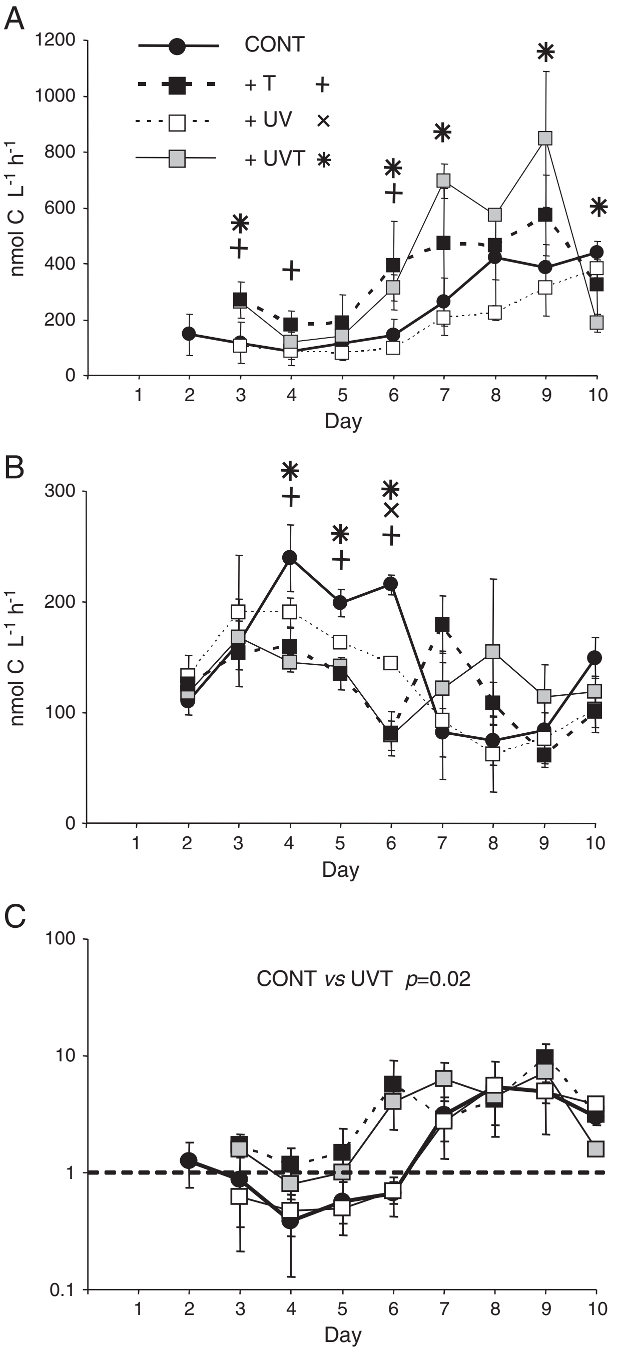

Fig. 4. Primary production (A) and bacterial production (B) and the PP:BP ration (C) in the UV, T and UVT mesocosms and the controls (CONT) (see Fig. 1 for details). Crosses and asterisks denote significant differences between the UV, T and UVT mesocosms and the controls (CONT). RM-ANOVA results are provided when differences were statistically significant ($p \leq 0.05$). The dashed line is the equivalence between PP and BP (ratio = 1).

The ratio between primary and bacterial C production (PP:BP ratio) (Fig. 4C) showed the same pattern for the UV mesocosms and for the controls, the values being less than 1 from day 3 to day 6 and greater than 1 thereafter. This ratio was significantly higher in the UVT mesocosms than in the controls (RM-ANOVA, $p = 0.02$) and rose to about 4 two days earlier than in the controls.

3.6. Cumulative microbial C and N losses

The microbial C and N losses calculated over the 9 days of the experiment were 40 and 6 μmol L^{-1}, respectively in the CONTmesocosms (Fig. 5A and B). After 9 days, the cumulative C and N losses were significantly higher (ANOVA, $p \leq 0.05$) in the mesocosms with increased temperature relative to the CONT mesocosms (+46% and +39%, respectively).

4. Discussion

4.1. Insignificant effect of increased UVBR

These experiments conducted in Thau lagoon clearly showed that increased UVBR did not have any significant effects on microbial C and N production (except on BP on one day). In their experiments on microbial communities in Thau lagoon using the same design for increased UVBR and temperature, Bouvy et al. (2011) also reported the responses of microbial components to simulated climatic variables, showing a small negative effect of a 20% UVBR increase in terms of abundance and activity. These observations do not appear to correspond to previous studies reporting significant negative effects of UVBR on photosynthesis and primary C production (Mousseau et al., 2000 and references therein) and bacterial activity (Herndl et al., 1993; Jeffrey et al., 1996a, 1996b; Chatila et al., 2001). The use of a realistic experimental design in this study may be the main reason for this discrepancy. The 20% UVBR increase applied here was corrected automatically with respect to variations in the natural UVBR (Nouguier et al., 2007) which was

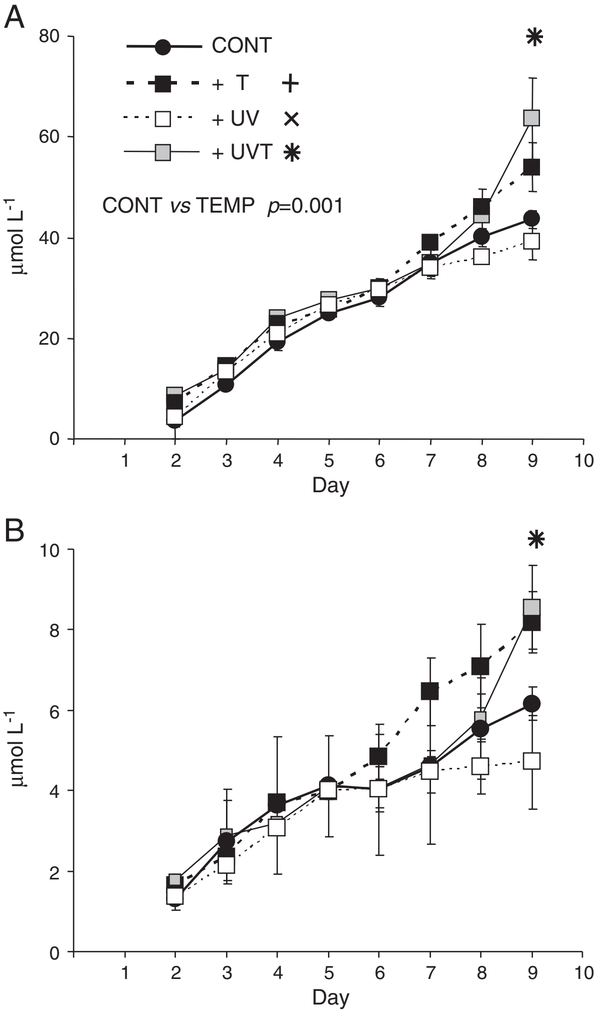

Fig. 5. Cumulative carbon (A) and nitrogen (B) losses calculated in the UV, T and UVT mesocosms and in the controls (CONT) (see Fig. 1 for details). Crosses and asterisks denote significant differences between the UV, T and UVT mesocosms and the controls (CONT). RM-ANOVA results are provided when differences were statistically significant ($p \leq 0.05$).

more realistic than the constant additional UVBR, independent of natural variations, which was usually used in previous studies.

The lower effect of UVBR on primary carbon production may also be explained by the development of efficient photoprotective mechanisms by phytoplankton when UVBR is reduced (during the afternoon). Similarly, bacterioplankton may activate various repair strategies against UVBR (Joux et al., 1999). It is, therefore, possible that the Mediterranean phyto- and bacterioplankton communities in this study were not very sensitive to the 20% increase in UVBR or that they acclimated very quickly to the increase in UVBR. The insignificant effect of UVBR observed here could also be due to the high variability measured within replicates which reduced the significance of differences obtained in this study. In future experiments dealing with Mediterranean microbial communities, the number of replicates should be increased to reveal any moderate UVBR effects on pelagic systems already submitted to high natural UVBR.

4.2. Dominance of warming on the microbial C and N production and losses

Warming had opposite effects on phytoplankton and bacteria. On the one hand, warming increased primary production (PP) with significantly higher inorganic carbon uptake (from 10% to more than 100% increase) on three occasions (Fig. 4A). On the other hand, the bacterial production (BP) was reduced by an average of 30% (range: 6%–63%) under warming. The reduction of BP appeared to be due to the decrease in bacterial abundance from a trophic cascade effect under warming that was observed during the same experiment (Vidussi et al., 2011). Half-way through the experiment, warming prompted the emergence of metazooplankton (copepod adults) which feed on ciliates and was, therefore favorable to heterotrophic nanoflagellates which graze on bacteria (Vidussi et al., 2011). The strong grazing pressure on bacteria under warming may have reduced competition with phytoplankton for inorganic nutrients and may have encouraged the development of the phytoplankton community. In this experiment, the ratio between autotrophic and heterotrophic C production (i.e. PP:BP ratio) was generally greater than 1 in mesocosms with increased temperature (Fig. 4C). However, PP:BP ratios were similar (ca. 4) after a few days irrespective of the experimental conditions, suggesting that warming did increase production rates within a range of nutrient availability which was equivalent in all the mesocosms. Combining an increase in UVBR with warming in this experiment did not have a more pronounced effect on the PP:BP ratio than that observed for warming alone. This suggests a dominant effect of warming on auto- and heterotrophic processes. No significant effect of climatic stressors was observed on microbial N uptake rates during the experiment. This may be due to the probable reduction of bacterial N uptake rates with the reduction in BP under warming being balanced by the increase in primary N uptake rates with the increase in PP under warming.

An earlier onset of the phytoplankton bloom under warming with an acceleration of ca. 1 day/°C was also observed during an indoor 30 day mesocosm experiment in Baltic sea water (Wohlers et al., 2009). However, it is generally assumed that a rise in ambient temperature is likely to affect bacterial production, respiration and growth efficiency (Vazquez-Dominguez et al., 2007; Sarmento et al., 2010). The variety of trophic levels involved in this study (all organisms $<1000\ \mu m$) together with the high activity of microorganisms usually reported in Thau lagoon (Bec et al., 2005; Collos et al., 2005) may explain discrepancies with previous studies which were performed on a simpler food web or in colder waters. The reduction in BP under warming observed in this study was probably due to greater control on bacteria abundances by heterotrophic nanoflagellate grazing pressure.

Primary production increased in the T and UVT mesocosms more than bacterial production decreased but, surprisingly, there was no observed increase in POC and PON concentrations as would be expected. This suggests that larger C and N losses (ca. +40%) occurred with increased temperature (T and UVT mesocosms) . The C:N ratio of these losses averaged 7 in all the mesocosms suggesting that they were by phytoplankton. Therefore, newly produced phytoplankton biomass sinking to the bottom of the mesocosms, despite the mixing by pumps, may mainly explain the C and N losses reported here, as also reported in other mesocosm studies (Wohlers et al., 2009; Taucher et al., 2012). Furthermore, Vidussi et al. (2011) clearly showed that the metazooplankton abundance increased at higher temperatures during the same experiment. The POC and PON measurements may not be representative of the large-sized plankton community, as copepods may have swum away and escaped from sampling, for example. Therefore, the greater C and N losses measured under warming may reflect not only a larger settled phytoplankton biomass but also greater transfer to the higher trophic levels.

5. Conclusions

These experimental results show firstly that the realistic simulated UVBR increase did not significantly affect the microbial C and N production in the Mediterranean coastal waters and that, secondly, warming alone or combined with increased UVBR had a major effect on C and N production in the microbial community in these waters. The main short-term consequence of warming was an earlier shift of the autotrophic/heterotrophic C ratio toward autotrophy leading to higher C and N losses. The major consequence of such climatic conditions in the Mediterranean coastal waters is that autotrophic processes could be encouraged and may lead to more efficient C and N transfer to the higher trophic levels and settling to the deeper waters.

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