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ORIGINAL PAPER

Indicators for photoreactivation and dark repair studies following ultraviolet disinfection

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Abstract Repair of DNA in bacteria following ultraviolet (UV) disinfection can cause reactivation of inactivated bacteria and negatively impact the efficiency of the UV disinfection process. In this study, various strains of *E. coli* (wild-type, UV-resistant and antibiotic-resistant strains) were investigated for their ability to perform dark repair and photoreactivation, and compared based on final repair levels after 4 h of incubation, as well as repair rates. Analysis of the results revealed that the repair abilities of different *E. coli* strains can differ quite significantly. In photoreactivation, the log repair ranged from 10 to 85%, with slightly lower log repair percentages when medium-pressure (MP) UV disinfection was employed. In dark repair, log repair ranged from 13 to 28% following low-pressure (LP) UV disinfection. *E. coli* strains ATCC 15597 and ATCC 11229 were found to repair the fastest and to the highest levels for photoreactivation and dark repair, respectively. These strains were also confirmed to repair to higher levels when compared to a pathogenic *E. coli* O157:H7 strain. Hence, these strains could possibly serve as conservative indicators for future repair studies following UV disinfection. In addition, dimer repair by photoreactivation and dark repair was also confirmed on a molecular level using the endonuclease sensitive site (ESS) assay.

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Introduction

Ultraviolet (UV) disinfection is now highly regarded as an alternative to chlorination for drinking water treatment due to its excellent biocidal properties without the formation of harmful disinfection by-products such as trihalomethanes [10, 12, 27]. It is also a non-chemical process so that water parameters such as pH and temperature do not influence its disinfection performance. The extremely short contact times (ranging from seconds to a few minutes) as compared to that for chlorination have also contributed to its rising popularity as an alternative disinfectant. The main mechanism of UV disinfection lies in the ability of UV radiation to penetrate through the cell membranes of microorganisms directly to the deoxyribonucleic acids (DNA). Upon the absorption of energy from the radiation, the structure of the DNA is altered via the formation of *cis-syn* cyclobutane pyrimidine dimers [4, 20], which prevents the replication of the microorganisms so that they ultimately die off [8].

However, due to the presence of ultraviolet radiation from the sun in the natural environment, natural defense mechanisms have evolved in bacteria and other microorganisms, so that UV-inactivated microorganisms are able to reverse the UV-induced damage via repair pathways such as photoreactivation and dark repair, allowing the microorganisms to regain activity [4, 7, 9]. This reduces the efficiency of UV disinfection and has an adverse impact on the microbiological quality of the treated water. As such, photoreactivation and dark repair of microorganisms following UV disinfection have been studied quite

extensively in the last few decades [1, 3, 5, 17, 19, 21, 22, 28, 29], especially for the two most commonly used UV lamps—the low-pressure (LP) and medium-pressure (MP) mercury UV lamps. LP UV lamps are traditionally used in UV disinfection and emit monochromatic UV radiation at 254 nm, which is close to the optimum germicidal wavelength of 260 nm [4]. MP UV lamps were developed in the last decade and emit a broad spectrum of wavelengths in the UV radiation region ranging from 200 to 400 nm [14]. These lamps also have higher UV radiation intensity, so that fewer lamps are required to achieve the same level of disinfection as LP UV lamps [13]. As such, installations employing MP UV disinfection have also increased in recent years. In these studies, *Escherichia coli* is commonly employed as an indicator microorganism as it is easily propagated and detected in the laboratory. Its repair characteristics are also well known [28]. It was obvious in the studies that photoreactivation played a highly important role in reversing UV-induced damage [5, 26], with up to 80% of the pyrimidine dimers being monomerized [16]. Dark repair has been found to be less significant following UV disinfection, but it can occur in the distribution system after leaving the treatment plant, and should be studied. However, the various literature available have reported repair results for different strains of *E. coli* which may have different repair abilities, and thus it is difficult to make comparisons or draw concrete conclusions about *E. coli* repair. Moreover, the results have so far not been compared with that of pathogenic strains for which the indicators represent, especially the waterborne pathogenic *E. coli* O157:H7 strain which can cause bloody diarrhea and death and poses a severe public health risk [18, 25]. In order to ensure that the *E. coli* strains used in UV disinfection and repair studies are representative of that of pathogenic strains, an indicator strain should be identified. Also, many photoreactivation literature dealing with drinking water disinfection have investigated UV doses up to 20 mJ/cm^2 [16, 28], even though practical UV doses applied are usually around 40 mJ/cm^2. It would, therefore, be useful to have photoreactivation data of the indicator at such high UV doses.

Hence, this study aims to investigate the photoreactivation and dark repair properties of various *E. coli* strains with different microbiological characteristics. The repair abilities were compared based on the final levels of repair achieved in 4 h of light or dark incubation following UV disinfection, as well as the rate of repair, in order to identify a strain that can be used as a conservative indicator for repair studies after UV disinfection. In addition, photoreactivation following high UV doses and the DNA repair of one of the indicator strains following UV disinfection was also investigated at a molecular level.

Materials and methods

Bacteria strains

Escherichia coli was chosen for this study as its repair characteristics are well known and it is commonly used as a bacteria indicator in disinfection studies. Four *E. coli* strains (ATCC 11775, 11229, 15597 and 700891) were purchased from the American Culture Type Collection, two strains (NCIMB 9481 and 10083) from the National Collections of Industrial, Marine and Food Bacteria and one strain (CCUG 29188) was purchased from the Culture Collection of the University of Göteborg. The microbiological characteristics of the *E. coli* strains are detailed in Table 1.

For each strain, an overnight phase was prepared by inoculating 1 mL of the frozen stock culture into 30 mL of tryptic soy broth (TSB) and shaking overnight at 37 ± 1 °C. One milliliter of this overnight culture was then added to 30 mL of fresh TSB and incubated in a shaker for 4 h at 37 ± 1 °C to obtain a log phase culture. The *E. coli* cells were harvested by centrifuging at 3,000×*g* for 10 min, washed twice with sterile 0.9% NaCl solution, and resuspended in 30 mL of sterile distilled water. This resulted in an *E. coli* concentration of approximately 1×10^9 CFU/mL. Just before UV irradiation, the suspension was diluted ten times with sterile distilled water to obtain a concentration of approximately 1×10^8 CFU/mL.

UV disinfection

The UV disinfection experiments were carried out in batch mode using a bench-scale collimated beam apparatus (Rayox® Model PS1-1-220, Calgon Carbon Corporation, USA), consisting of interchangeable low- (10 W) and medium-pressure (1 kW) mercury lamps. Ten milliliters of the prepared *E. coli* solution was dispensed into a 60-mm

Table 1 Characteristics of *Escherichia coli* strains used in the study

Escherichia coli strain	Characteristics/remarks
ATCC 11775	Type strain for *E. coli*
ATCC 11229	Commonly used in disinfection studies as indicator
ATCC 15597	Derived from *E. coli* K-12 strain, bacteriophage host
ATCC 700891	Contains *Famp* plasmid which confers ampicillin and streptomycin resistance, bacteriophage host
NCIMB 9481	Host for phage lambda
NCIMB 10083	Wild-type strain isolated from human feces
CCUG 29188	Attenuated strain belonging to the *E. coli* O157:H7 serotype

diameter Petri dish and then exposed to UV radiation for a pre-determined exposure time to achieve the required UV dose, which will provide a 5-log reduction in the *E. coli* concentration. The exposure times were calculated based on the UV doses required and the average intensity of the radiation incident on the water sample, and taking into account the various factors that can affect the measured UV intensity such as Petri-, water-, sensor factor, etc. [2, 28]. These factors correct for the variation of the UV intensity across the surface of the bacteria solution and along the depth of the water, as well as correction for errors in the UV sensor used to measure the UV intensity. All the bacteria samples were magnetically stirred with a spin bar (10 mm × 3 mm) throughout the irradiation process. Immediately after irradiation, 0.5 mL of the irradiated bacteria was extracted for the determination of bacteria concentration, while the rest of the sample was covered and used for photoreactivation and dark repair studies within 3 min of irradiation.

Photoreactivation and dark repair

For photoreactivation, the Petri dishes containing the irradiated *E. coli* suspensions were placed on magnetic stirrers and stirred continuously while being exposed to a light intensity of about 11.5 kLx for up to 4 h using a 20 W fluorescent light (National, Matsushita Electrical Industrial Co. Ltd, Japan). The light intensity was measured using a digital luxmeter (Model E2, B. Hagner AB, Sweden) and samples were taken at hourly intervals for the determination of the *E. coli* concentrations. The same procedures were adopted for dark repair, except that the Petri dishes were placed on magnetic stirrers in the dark, and were also covered with aluminum foil to prevent accidental exposure of samples to light during sample collection. The temperature for the repair experiments was maintained at 23 ± 1 °C. All experiments were conducted thrice to ensure reproducibility.

Bacteria enumeration

The determination of the *E. coli* concentrations was performed using the spread plate method in accordance to the Standard Methods [24]. Briefly, samples were serially diluted using sterile 0.9% NaCl solution, plated in duplicate on tryptic soy agar (TSA) and incubated for 24 h at 37 ± 1 °C. After incubation, the plates were counted and the counts were averaged and recorded as CFU/mL.

Data analysis

Due to the fact that the initial *E. coli* concentrations can vary from day to day, and that the application of the same UV dose does not exactly lead to 5-log reduction in bacteria counts, the following formula was applied to the bacteria counts at each hour:

$$\%\ \text{repair} = \frac{N_t - N_0}{N_{\text{initial}} - N_0} \quad (1)$$

where N_t is the concentration of *E. coli* at time of exposure, t, to repair conditions (log CFU/mL), N_0 is the concentration of *E. coli* immediately after UV disinfection (log CFU/mL), and N_{initial} is the initial concentration of *E. coli* before UV disinfection (log CFU/mL).

This equation is similar to that proposed by Lindenauer and Darby [11], except that log concentrations are used here. The use of Eq. 1 allows the light and dark repair of each *E. coli* strain at each time interval to be expressed in terms of percentage repair, per unit log reduction. Such a normalization method removes the effects of varying initial *E. coli* concentrations and the intrinsic variations in log-reductions during the experiments, so that the results can be compared on an equal basis.

In addition, the data was also analyzed to obtain the rate of repair. This is used to differentiate and compare between two or more *E. coli* strains which may have the similar levels of repair at the end of the experiments. Based on photoreactivation curves obtained, most of the repair was achieved within the first two hours, followed by leveling off of the photoreactivation curves after that. Hence, for meaningful comparisons, the rate of repair was calculated based on the amount of repair within the first hour using the following equation [3]:

$$\text{Rate of repair } (\log\ \text{h}^{-1}) = \frac{N_1 - N_0}{t} \quad (2)$$

where N_1 is the concentration of *E. coli* after 1 h of exposure to repair conditions (log CFU/mL) and t is the time interval between the two samples (taken to be 1 h).

Molecular level detection of DNA repair

The endonuclease sensitive site (ESS) assay used by Oguma et al. [16] was used to determine the level of damage in the DNA of the *E. coli* cells. Briefly, DNA was extracted from 30 mL of *E. coli* cells and then cleaved at the pyrimidine dimer sites using T4 endonuclease V (Trevigen, USA). The sample was then analyzed using alkaline gel electrophoresis and a gel documentation software (Quantity One® 1-D analysis software, Bio-Rad Laboratories, USA) was used to obtain the median molecular length of the DNA. Samples were analyzed before and after UV irradiation, and at one and four hours after irradiation.

Results and discussion

UV inactivation of *Escherichia coli*

Figure 1 shows the inactivation of the various *E. coli* strains following LP and MP UV disinfection at different doses. It is evident that there is a wide range of responses to both types of UV radiation for the different *E. coli* strains, with a 4-log reduction requiring UV doses ranging from 6 to 13 mJ/cm^2 for LP UV radiation and 4.5 to 9 mJ/cm^2 for MP UV radiation. Moreover, the shapes of the inactivation curves shown in Fig. 1 are similar to the shouldered survival curves from Harm [4]. This suggests that the inactivation kinetics of *E. coli* belong to the multi-hit or multi-target case, where the effectiveness per unit UV dose increases as the UV dose increases.

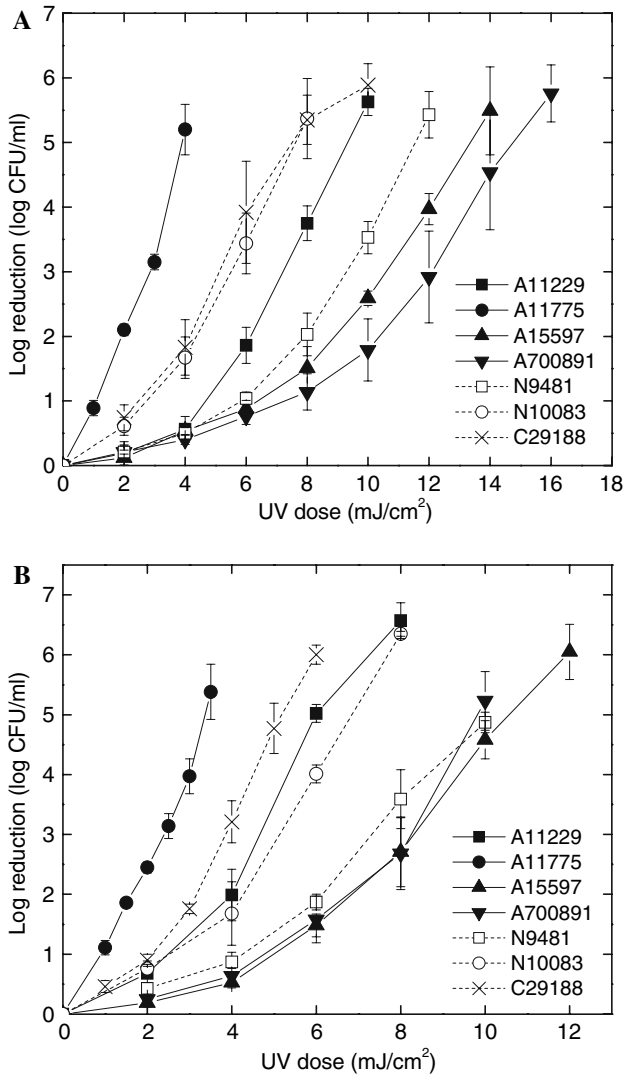

Fig. 1 UV inactivation of various *Escherichia coli* strains (A: ATCC, N: NCIMB, C: CCUG) by **a** LP and **b** MP UV disinfection. *Error bars* represent standard deviations of three to five experiments

Based on the data in Fig. 1, the most UV-resistant strains are the bacteriophages (ATCC 15597 and ATCC 700891). This concurs with the findings of Mofidi et al. [15] who reported that ATCC 15597 was more UV resistant than other *E. coli* strains, including the type strain ATCC 11775. In addition, the inactivation data for ATCC 11229 and NCIMB 10083 also agree with those previously reported for stationary phase cells [5, 16, 23]. Of all the strains tested in the study, the wild-type strain (NCIMB 10083) and the attenuated O157:H7 strain (CCUG 29188) exhibited the greatest susceptibility to UV disinfection. Hence, ATCC 11229, the strain commonly used for disinfection studies, should adequately serve as a disinfection indicator for *E. coli* O157:H7 and other *E. coli* strains that are present in the environment. However, Sommer et al. [23] found that other pathogenic *E. coli* strains (e.g. serotypes O25 and O78) are more UV-resistant than ATCC 11229. As such, it might be better to select a more conservative indicator such as ATCC 15597 or ATCC 700891 for future studies on UV disinfection.

Based on the data in Fig. 1, it was also found that lower UV doses were required to achieve the same log reduction of all *E. coli* strains when MP UV radiation was employed, indicating that MP UV disinfection was more efficient than LP UV disinfection. This has been reported previously [6], and is likely due to the more intense radiation and broader wavelength spectrum emitted by MP UV lamps that caused damage to intercellular biomolecules other than DNA [9].

Photoreactivation of *Escherichia coli* following UV disinfection

The photoreactivation results (in terms of percentage log repair) of the various *E. coli* strains following LP and MP UV disinfection are presented in Fig. 2. For most of the strains in the study, the photoreactivation curves follow a similar trend, where much of the repair takes place within the first two hours of repair, followed by leveling off of the curves after that. This trend is consistent with those reported previously [16, 19, 28]. In this study, the maximum level of photoreactivation achieved was about 85% of the total number of the inactivated bacteria. This agrees with the data from Oguma et al. [17] who observed about 84% repair of pyrimidine dimers in *E. coli* after LP UV disinfection, and suggests that some of the UV-induced damage is irreparable via photoreactivation. Nevertheless, this is a significant level of repair, i.e., for every 5 $\log_{10}$ inactivation of bacteria, up to 4.25 $\log_{10}$ of the inactivated bacteria can reactivate and re-contaminate the water. Therefore, exposure of UV-disinfected water to light should be avoided to ensure that photoreactivation does not occur. For MP UV disinfection, photoreactivation levels of

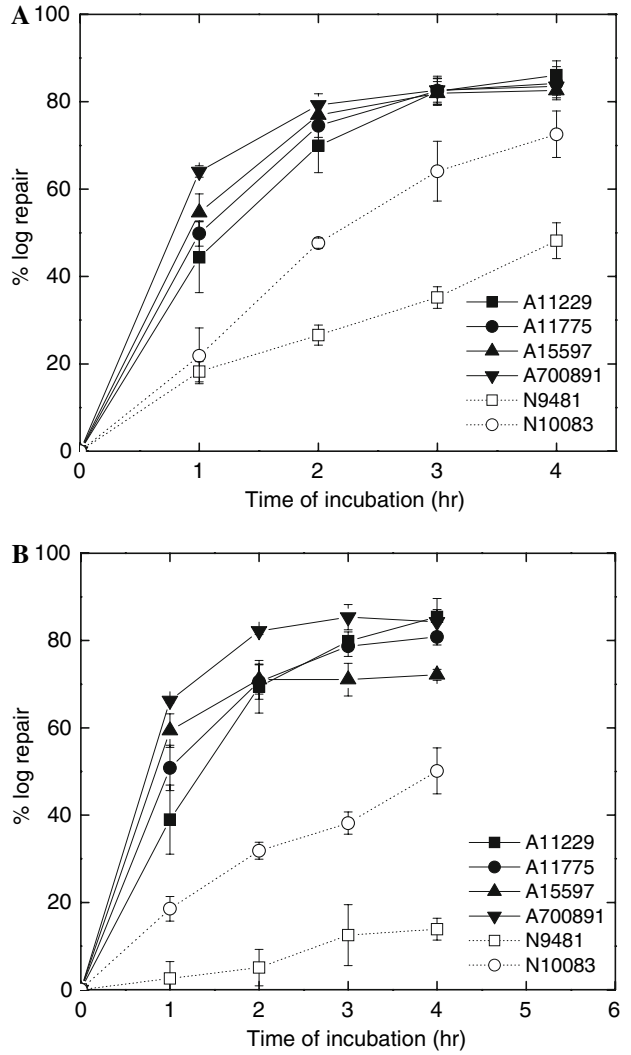

Fig. 2 Percentage log repair of various *E. coli* strains (A: ATCC, N: NCIMB) after exposure to fluorescent light following **a** LP and **b** MP UV disinfection. *Error bars* represent standard deviations of three to five experiments

up to 80% were observed in Fig. 2b. In comparison, a previous study conducted on *E. coli* ATCC 11229 (stationary phase culture) and IFO 3301 (also known as NCIMB 10083) concluded that minimal photoreactivation occurred with MP UV disinfection [16, 28]. The difference between the conclusions of the previous studies and the current one may be because of the use of log phase cultures in the current study, where the cells were actively dividing and were therefore in an energetically active state to achieve higher levels of repair. It can also be seen that two strains (NCIMB 9481 and NCIMB 10083) were unable to achieve complete photoreactivation even with up to 4 h of exposure to fluorescent light following both LP and MP UV disinfection. One possible reason for this is that these strains may have less efficient photoreactivation mechanisms or fewer photoreactivation enzymes so that repair was slower. Hence, *E. coli* NCIMB 9481 and NCIMB 10083 should not be used for photoreactivation studies as they tend to underestimate the photoreactivation levels of pathogens.

In order to identify an appropriate strain for photoreactivation studies, the various strains were compared using the rate of repair as shown in Fig. 3. Among the various *E. coli* strains, the repair rates of ATCC 15597 and ATCC 700891 were the highest following LP UV radiation, with repair rates of approximately 3 and 3.25 log h^{-1}, respectively. The same can also be observed following MP UV radiation, where these two strains also demonstrated the greatest UV resistance (Fig. 1). This is not surprising as bacteria cells are continuously repairing the UV-induced damage even as they are being formed during UV disinfection [5]. As such, the cells with the most efficient repair mechanisms would be able to better resist the effects of UV radiation. It suggests that the strains more resistant to UV radiation are likely to achieve higher repair levels. Such strains should therefore serve as indicators for photoreactivation studies since they are non-pathogenic as well. As shown in Table 1, *E. coli* ATCC 15597 is a derivative of the commonly studied K-12 strain, and so its biological and physical characteristics are well-understood. *E. coli* ATCC 700891, even though it has a slightly higher repair rate than ATCC 15597 does, contains the Famp plasmid which encodes for ampicillin and streptomycin resistances. The presence of this plasmid may have some effects on its high UV resistance and efficient repair mechanism, which may be affected should the plasmid be lost during replication or growth. As such, ATCC 15597 is a better option as a conservative indicator

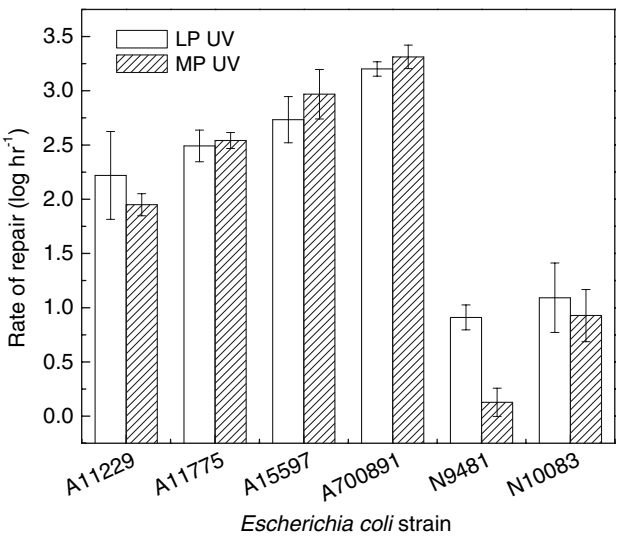

Fig. 3 Photoreactivation rates of various *E. coli* strains (A: ATCC; N: NCIMB) following LP and MP UV disinfection. *Error bars* represent standard deviations of three to five experiments

for future photoreactivation studies, where UV irradiation and photoreactivation conditions used may be considerably different from those in the current study and may thus affect the UV resistance and repair abilities of *E. coli* ATCC 700891.

Dark repair of *Escherichia coli* following UV disinfection

The dark repair levels of the various strains of *E. coli* tested in this study are presented in Fig. 4. It is evident that dark repair levels are much lower than that for photoreactivation, with a maximum of 25% log repair achieved after LP UV disinfection and 4 hours of incubation in the dark. This is 3.4 times lower than that achieved with photoreactivation, and concurs with previous findings using *E. coli* ATCC 11229 [28], ATCC 15597 [15] and NCIMB 10083 [16]. There also appears to be leveling off of dark repair levels after about 2 h for some strains after LP UV disinfection, and 1 h after MP UV disinfection. This demonstrates that MP UV disinfection may have a more significant impact on dark repair mechanisms. It is also interesting to note that for NCIMB 9481, the bacteria concentration decreased during incubation following MP UV disinfection, indicating that MP UV radiation which has a broad wavelength spectrum may have induced some delayed mutagenic effects in the cells which continued to kill the cells after disinfection.

With the exception of *E. coli* NCIMB 9481 exposed to MP UV disinfection, all other strains in this study exhibited dark repair to a certain extent. Previous research by Oguma et al. [16] and Zimmer and Slawson [28] concluded that dark repair does not occur with IFO3301 (NCIMB 10083) and ATCC 11229, respectively, following LP and MP UV disinfection. Again, this difference in results might be due to the use of bacteria cells in different growth phases. The current study used log phase cultures, where the actively dividing cells may have more energy and greater ability to respond quickly to UV damage via dark repair mechanisms, instead of stationary phase cells, which were used in the other two studies.

It is clear from Fig. 4 that ATCC 11229 achieved the highest level of dark repair following LP UV disinfection, and its dark repair level was similar to that of ATCC 11775 and lower than ATCC 700891 after MP UV disinfection. The dark repair rates also confirm this trend (data not shown). Taking into account the results from both LP and MP UV disinfection, ATCC 11229 would be the most suitable indicator for dark repair studies. Since it is also a disinfection indicator commonly used in UV disinfection studies, it will therefore also be convenient to adopt this strain for future dark repair research.

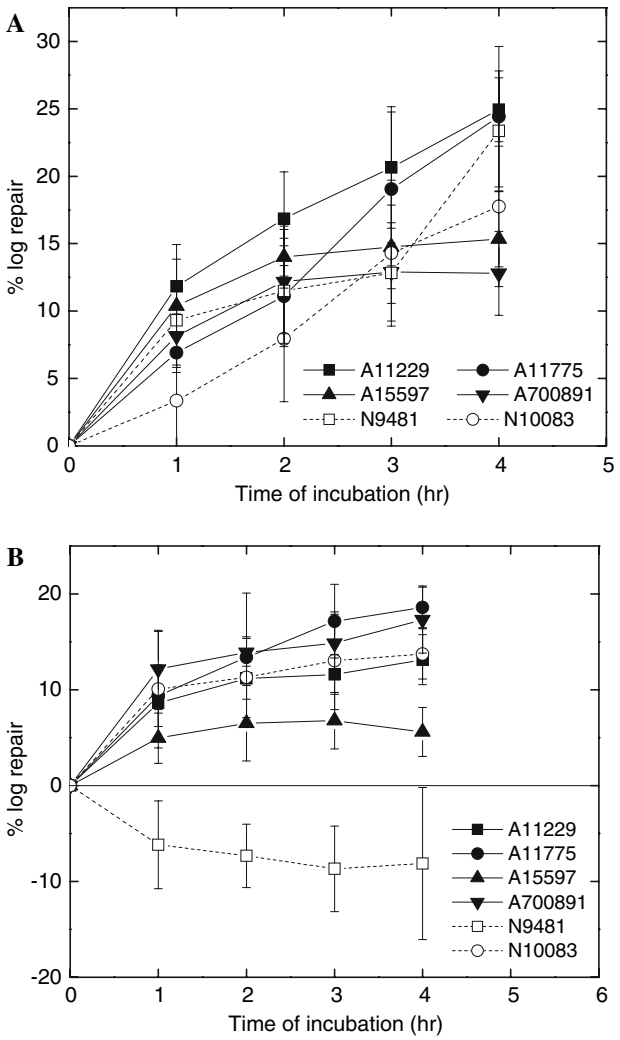

Fig. 4 Percentage log repair of various *E. coli* strains (A: ATCC, N: NCIMB) after incubation in the dark following **a** LP and **b** MP UV disinfection. *Error bars* represent standard deviations of three to five experiments

Repair of selected indicators and *E. coli* O157:H7

Having identified *E. coli* ATCC 15597 and ATCC 11229 as indicators for photoreactivation and dark repair studies, respectively, the repair abilities of each of these strains were tested against the attenuated O157:H7 strain (CCUG 29188) for their suitability as indicators. In order to mimic practical disinfection conditions, the same UV doses were applied to the three *E. coli* strains studied here, and then incubated in the light (ATCC 15597 and CCUG 29188) or dark (ATCC 11229 and CCUG 29188). The results are presented in Fig. 5.

Based on the results in Fig. 5, it is apparent that regardless of the lamp type and UV doses applied, the final concentrations of the indicator bacteria for photoreactivation and dark repair after UV disinfection followed by incubation for repair were always similar to, or higher than,

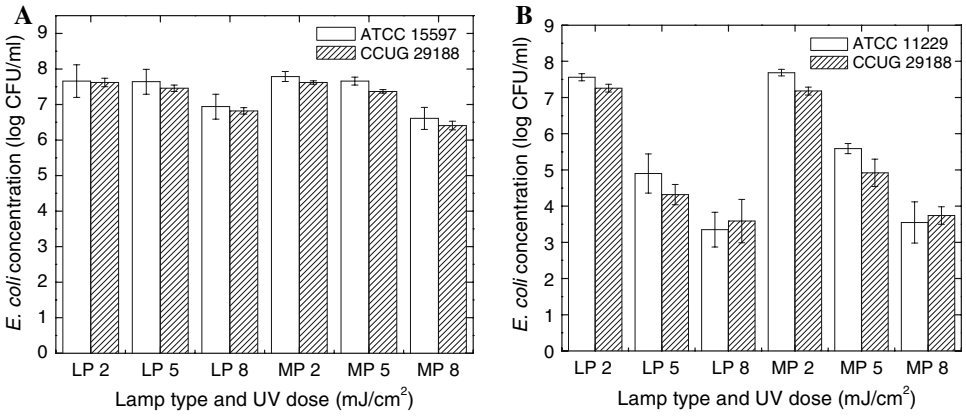

Fig. 5 Comparisons of the final log concentrations of *E. coli* O157:H7 and selected indicator strains following exposure to **a** fluorescent light and **b** dark conditions after LP and MP UV disinfection at various UV doses. Standard deviations of three to five experiments are presented as *error bars*

that of the *E. coli* O157:H7 strain. This thus confirms that these two strains are suitable for use as photoreactivation and dark repair indicators for repair studies after UV disinfection, and that they are also applicable for different UV lamp configurations and a range of UV doses. It is recommended that these selected strains be adopted so that conclusions between different repair studies can be meaningfully compared and discussed without having to consider the variation in biological characteristics that exist between different strains of the same bacterial species.

Photoreactivation of *E. coli* ATCC 15597 at high UV doses

Escherichia coli ATCC 15597 was exposed to LP and MP UV doses of 20, 40 and 60 mJ/cm^2 to investigate its photoreactivation abilities at high UV doses and the results are presented in Fig. 6. No data is shown for photoreactivation following LP and MP UV irradiation at 60 mJ/cm^2 as no colonies could be detected on the agar plates. Thus, there is no photoreactivation observed at this UV dose. Nevertheless, it is clear that at the other two UV doses tested, photoreactivation following MP UV disinfection (dashed lines) was always lower than that following LP UV disinfection (solid lines). This is consistent with previous reports [13, 16, 23], and is likely because of possible damage to the other biomolecules caused by the wide spectrum of wavelengths in MP UV irradiation. Photoreactivation is evident even at UV doses as high as 20 and 40 mJ/cm^2, although the final bacteria concentrations were much lower. For example, *E. coli* photoreactivated to a final concentration of about 7-log CFU/mL following a LP UV dose of 8 mJ/cm^2 (Fig. 5a), but only to 4.5-log and 3-log CFU/mL after exposure to LP UV doses of 20 and 40 mJ/cm^2, respectively. This is indicative of the lower repair ability by *E. coli* with increasing UV dose exposure. The results therefore suggest that in order to completely eliminate photoreactivation from taking place, UV doses of

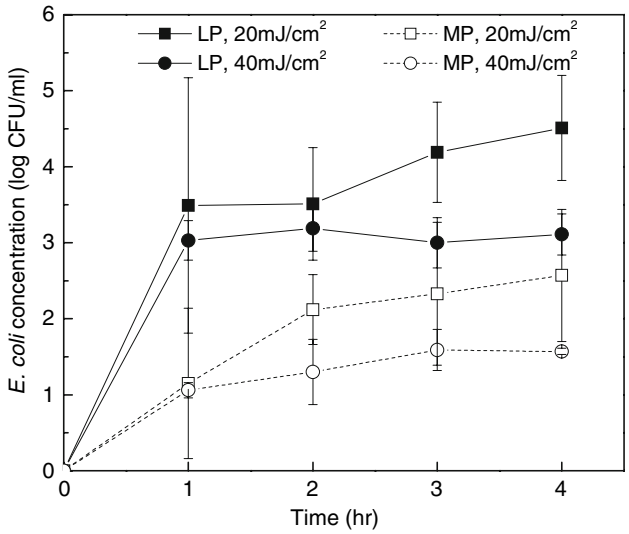

Fig. 6 Increase in *E. coli* ATCC 15597 concentrations with time of exposure to fluorescent light following LP and MP UV disinfection at high UV doses. Standard deviations of three to five experiments are presented as *error bars*

60 mJ/cm^2 or higher should be applied for UV disinfection of drinking water, and that treated water should not be exposed to light following UV disinfection.

Photoreactivation of *E. coli* ATCC 15597 using ESS assay

Other than the cellular study, the ESS assay [16] was used to investigate photoreactivation and dark repair on a molecular level. *E. coli* ATCC 15597 was exposed to LP and MP UV doses of 1 and 5 mJ/cm^2 and exposed to either fluorescent light or kept in the dark. The results of the ESS assay are presented in Fig. 7.

It can be seen that the median molecular lengths decreased following both LP and MP UV disinfection, and then increased with time of exposure to fluorescent light or incubation in the dark. When exposed to UV radiation,

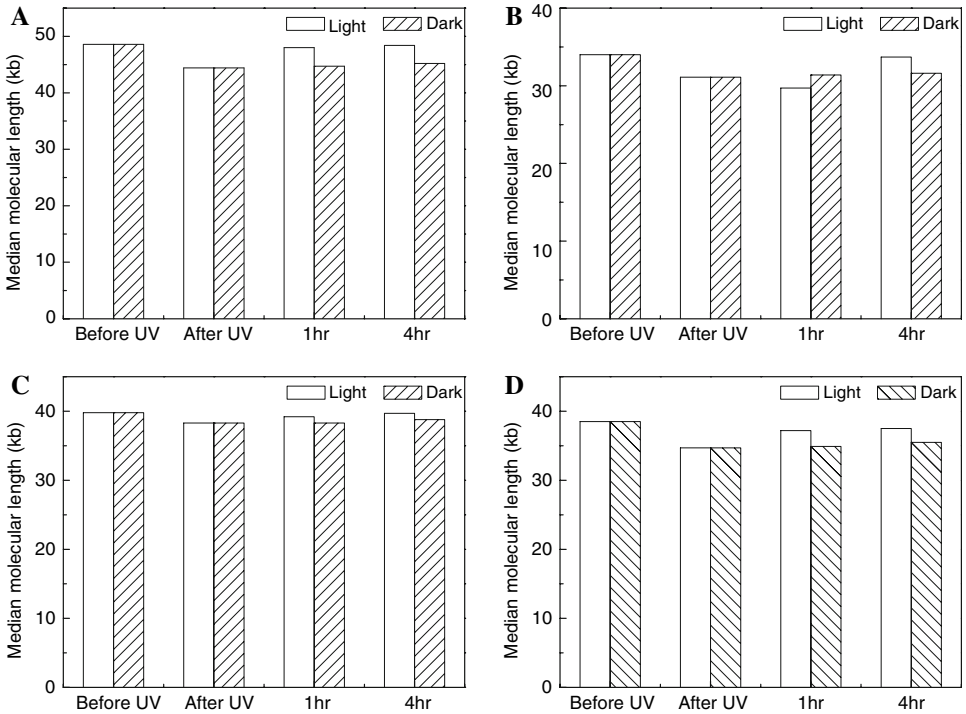

Fig. 7 Changes in median molecular length of *E. coli* ATCC 15597 DNA with exposure to LP UV doses of **a** 1 mJ/cm^2, **b** 5 mJ/cm^2 and MP UV doses of **c** 1 mJ/cm^2 and **d** 5 mJ/cm^2, followed by incubation under fluorescent light or in the dark for up to 4 h. Data presented are from a single experiment

pyrimidine dimers are formed in the DNA, so that the action of T4 endonuclease V cleaves the DNA into many small parts where the dimers are present. This results in smaller fragments of DNA when gel electrophoresis is applied to UV irradiated DNA. With time, the dimers are removed via photoreactivation or dark repair, so that the median molecular lengths gradually increase. It was observed that despite the existence of repair mechanisms, the molecular lengths were never fully repaired to that of the initial DNA (i.e., before UV irradiation), suggesting that some dimers are not repaired within the duration of the experiments. Nevertheless, the increasing median molecular lengths suggest that dimers were continuously being removed from the DNA during incubation after UV disinfection. In addition, the data in Fig. 7 shows that the median length of DNA was higher after four hours of exposure to light than incubation in the dark, for all UV lamps and doses tested. This suggests that greater dimer repair was achieved in the presence of light. Even though the data in Fig. 7 is from one experiment, the trends observed here nevertheless agree with those observed in the cellular study, and also confirms that the removal of dimers is directly related to the increase in bacteria concentrations observed in Figs. 2 and 4.

Conclusions

In conclusion, this study investigated the photoreactivation and dark repair abilities of several strains of *E. coli* following LP and MP UV disinfection. A wide range of UV resistances were observed among the various *E. coli* strains. Photoreactivation and dark repair abilities were also found to differ greatly among them. Based on final repair levels and rates of repair obtained in this study, *E. coli* ATCC 15597 and *E. coli* ATCC 11229 were identified as the photoreactivation and dark repair indicators, respectively, and were suggested to be used in future studies for more meaningful comparisons across different studies. In addition, *E. coli* ATCC 15597 has demonstrated its ability to be used for photoreactivation studies at high UV doses and also for dimer repair studies at the molecular level using the ESS assay, which served as confirmation that DNA repair was taking place at the cellular level.

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