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RESEARCH ARTICLE

A novel *Oocystis algal* strain enables highly efficient simultaneous biodegradation of bisphenol A and carbon capture in seawater

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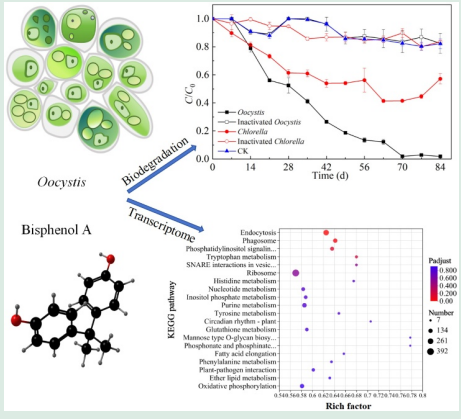
HIGHLIGHTS

- *Oocystis* obtained high BPA removal rate and carbon capture rate.
- SOD/POD activity of the *Oocystis* was much higher than that of the *Chlorella*.
- The engagement of POD and photosynthesis damage occurred during BPA biodegradation.
- BPA could serve as growth promoter for *Oocystis* during the BPA removal process.
- BPA was mainly removed through hydroxylation, demethylation, and conjugation.



ABSTRACT: The removal of bisphenol A (BPA) in seawater using microalgae is still a challenge due to the low removal efficiency and weak tolerance. A novel *Oocystis algal* strain was isolated for BPA removal with an efficiency (> 98%) over two times higher than that of the common microalgae *Chlorella* (42.8%). The maximal carbon capture rate of *Oocystis* was 0.16 g/(L·d) which was much higher than that of *Chlorella* (0.06 g/(L·d)). The BPA removal fitted a first-order kinetic model and *Oocystis* showed a maximum removal rate of 29.80 μg/(L·d) at a BPA concentration of 2000 μg/L. The new *Oocystis* strain had a wide range of pH adaptability for BPA removal. The sharp increase in peroxidase (POD) activity indicated its involvement in BPA degradation. Transcriptome analysis showed that BPA mainly affected the photosynthesis-related genes while the engagement of glutathione POD in the BPA biodegradation was confirmed. BPA could also serve as growth promoter for *Oocystis* during the removal process, which subsequently enhanced the growth and carbon capture. BPA could be removed by the *Oocystis* strain through hydroxylation, demethylation, and conjugation. The *Oocystis* strain still maintained high BPA removal efficiency (100%) and carbon capture rate (0.2 g/(L·d)) in the pilot-scale

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tailwater treatment system, illustrating microalgal processes were efficient for marine pollution control. This study also provides new ideas for developing low-cost carbon capture technologies to achieve the goal of carbon neutrality.

KEYWORDS: *Oocystis*, Micropollutant, Stress response, Degradation, Transcriptome analysis, Carbon capture

1 Introduction

As an important precursor compound in the polymer industry, bisphenol A (BPA) is widely used in the manufacture of plastics, pesticides, coatings, flame retardants, epoxy resins, polycarbonate, and other chemical products (Chen et al., 2016; Zhao et al., 2023). BPA can enter water bodies through sewage discharge, surface runoff and landfill seepage. BPA has been detected in rivers, lakes, drinking water, and sewage treatment plants (Lu et al., 2015; 2024; Jia et al., 2021; Bai et al., 2024). BPA, a kind of environmental hormone, can interfere with the nervous and immune systems of organisms, disrupt the normal function of the endocrine system, and have strong teratogenic, carcinogenic and mutagenic effects (Khan et al., 2021; Zhang, 2023b; Niavarani et al., 2024). BPA can be concentrated by aquatic organisms to threaten the ecosystem, the safety of drinking water, and human health (Xiong et al., 2016a; Wu et al., 2022). Therefore, it is particularly important to develop efficient methods for the removal of BPA from wastewater. Physical, chemical, and biological methods have been widely used to remove BPA from wastewater (Usman et al., 2021; Zhang et al., 2021; Hou and Yang, 2022). Biological methods have been regarded as a promising approach for removing BPA in wastewater due to their eco-friendliness and economic advantages (Xiong et al., 2017; Cao et al., 2020). Bacteria (*Bacillus subtilis*, *Lactobacillus plantarum*, *Saccharomyces cerevisiae*) and fungi (*Trametes versicolor*) have been applied to the biodegradation of BPA, but they were slightly inferior to microalgae due to harsh culture conditions or lower removal rate (Loffredo et al., 2012; Kyrila et al., 2021). Microalgae have good potential for removing harmful substances from the environment (Zhang et al., 2023a; Helal et al., 2024; Zheng et al., 2024). Previous studies reported the interaction between BPA and algae (Ben Ali et al., 2021; Lu et al., 2022; Azizullah et al., 2022). About 88% of BPA with initial concentration of 0.01 mg/L was removed by marine microalga *Stephanodiscus hantzschii* within 16 d (Li et al., 2009). *Chlorella fusca* could remove 85% of BPA from an aqueous solution containing 40 μmol/L BPA within 120 h under photosynthetic autotrophic conditions (Im and Löffler, 2016) while *Graesiella*/*Picocystis* could adsorb (6%–12%)/(5%–12%) of BPA (Ben Ouada et al., 2018b). Moreover, *Chlamydomonas* and *Ulva pertusa* were also confirmed to remove BPA (Zhang et al., 2021; Carbó et al., 2023). However, the low removal efficiency of BPA (Ji et al., 2014; Eio et al., 2015; Wang et al., 2017; Ben Ouada et al., 2018a; Zhang et al., 2019) has hindered the wide application of microalgae for the removal of BPA.

The removal of BPA in seawater system using microalgae with high efficiency was still a challenge. As a genus of dominant planktonic green algae in the subtropical area, *Oocystis* can adapt to a wide range of temperature and salinity to widely distribute in shrimp aquaculture ponds, estuaries and other areas. *Oocystis* could effectively reduce the concentrations of ammonia nitrogen and nitrite nitrogen in aquaculture water bodies (Liu et al., 2020). Therefore, *Oocystis* might be effective in remediating BPA pollution. This study reported novel *Oocystis* strain with the ability to remove BPA in seawater with high efficiency. The aim of this study is to obtain initial information on the simultaneous biodegradation of BPA and carbon capture using the novel *Oocystis* strain. The findings of this study will provide new perspectives for remediating BPA-contaminated water by using microalgae.

2 Materials and methods

2.1 Chemicals and reagents

BPA was purchased from Shanghai Macklin Biochemical Co., Ltd. (China) with a purity greater than 99%. BPA was dissolved in HPLC-grade methanol (Merck, Germany) to prepare a 1 g/L stock solution and stored at 4 °C.

2.2 Isolation, purification, cultivation, and identification of microalgae

The green algae strain YTLJ-NAPE-RC3 (GenBank accession number PQ932029) belonging to the genus *Oocystis* according to its 18S rDNA analysis (Fig. S1) was isolated from the coastal water of Shandong Province, China. The microalgae were purified and

isolated on f/2 solid medium (15–25 g/L agar) (Guillard, 1975). The algal culture was inoculated aseptically onto solid medium using the coated plate method with the coated dishes incubated upside down at 20 °C in a thermostatic light incubator. The visible strips or clumps of algal cells were picked out in the liquid medium with an inoculation ring after they grew on the petri dish while the algae seeds were kept in a constant temperature incubator at 10 °C. A commercial marine *Chlorella* strain (*Chlorella* sp. GY-H6) was purchased from Shanghai Guangyu Biological Technology Co., Ltd., China.

2.3 Experimental setup for biodegradation of BPA

All experiments were conducted in 250 mL conical flasks with three replicates. Each flask was periodically shaken 3 times a day while the position of flask was randomly adjusted to eliminate any systematic error caused by uneven light. The concentration of BPA was measured every 7 d to investigate the effects of initial BPA concentration, pH, temperature, salinity, inoculum amount, external carbon source and light intensity on the degradation of BPA. The experimental settings were detailed in Table S1. The effects of BPA on microalgae growth were measured by cell dry weight.

The bio-pilot scale tailwater treatment experiment was conducted in a 10-L fish tank filled with the tailwater of the eel and shrimp recirculating aquaculture system. *Oocystis* cells at logarithmic growth phase were inoculated into the BPA-spiked (50 μg/L) wastewater.

2.4 Analytical methods

The sample processing and BPA detection methods were shown in Table S2. The metabolites of BPA were subjected to analysis by using high-performance liquid chromatography-quadrupole time-of-flight mass spectrometry (HPLC-QTOF-MS, Waters HCLass XEVOG2XSQTof, Waters, USA) system equipped with a Waters SunFire C18 reverse-phase column. Separation utilized a gradient elution program with water and methanol as mobile phases, and the injection volume was set at 10 μL. Photosynthetic pigment content, MDA (malondialdehyde) concentration, and activities of antioxidative enzymes including POD (peroxidase), CAT (catalase), and SOD (superoxide dismutase) were determined according to previous study (Xiong et al., 2016b). RNA extraction, next-generation sequencing, and transcriptional analysis were conducted by Shanghai Majorbio Biotechnology Co. DEGs (differentially expressed genes) were functionally annotated using the GO (Gene Ontology) and KEGG (Kyoto Encyclopedia of Genes and Genomes) databases.

2.5 Data processing

All experiments were conducted in three parallel groups. One-way analysis of variance and Tukey's test were used to analyze significant differences and two-way comparisons of group means. The data were expressed by Mean±SD (n = 3). Different letters meant significant difference at 0.05 level. The data calculation methods for biodegradation rate and kinetics, and carbon capture rate were described in the supporting information in detail.

The biodegradation rate of BPA (%) was determined from the difference in concentration in the medium according to Eq. (1):

$$\text{BPA removal efficiency}\,(\%) = \frac{C_0 - C_t}{C_0} \times 100\%. \quad (1)$$

The BPA removal data were fitted by pseudo-first-order kinetic model (Eq. (2)) as follows:

$$-\ln\left(\frac{C_t}{C_0}\right) = k \times t, \quad (2)$$

where C_0 (μg/L) and C_t (μg/L) are the initial BPA concentration and residual BPA concentration at time t (d) in the aqueous solution, respectively; k (d^{-1}) represents the rate constant of the pseudo-first-order model.

The carbon capture rate was calculated using Eq. (3):

$$Rc = \frac{X_2 - X_1}{t_2 - t_1} \times m_{cbm} \times \frac{m_{CO_2}}{m_C}, \quad (3)$$

where X_2 and X_1 (g/L) correspond to the biomass at time t_2 and t_1 (d), respectively. Parameter m_{cbm} is the mass fraction of carbon determined in the microalgal biomass while m_{CO_2} and m_C (g/mol) are the molecular masses of carbon dioxide and carbon, respectively (Duarte et al., 2017).

3 Results and discussion

3.1 Removal kinetics of BPA by *Oocystis* sp. YTLJ-NAPE-RC3

The *Oocystis* sp. YTLJ-NAPE-RC3 had a BPA removal efficiency of 97.8% in 84 d while the BPA removal efficiency of the common freshwater green alga *Chlorella marine* was only 42.8%, confirming the superiority of *Oocystis* for BPA removal (Fig. 1). This process was fitted using the first-order kinetic model.

The reaction rate constant and half-life of *Oocystis* sp. YTLJ-NAPE-RC3 were 0.0321 d^{-1} and 21.6 d, respectively. The reaction rate constant and half-life of *Chlorella* reached 0.0147 d^{-1} and 47.4 d, respectively. The growth of *Oocystis* sp. YTLJ-NAPE-RC3 reached stationary phase after approximately 42 d from inoculation based on the change of dry microalgal cell weight with time. The dry cell weight (DCW) of *Chlorella* decreased sharply after 42 d due to the short-term growth cycle of the *Chlorella*. The *Oocystis* cells were oval with a diameter of 5–10 μm while the *Chlorella* cells were larger than *Chlorella* with a diameter of about 3–5 μm according to the scanning electron micrographs and confocal micrographs (Fig. S2). The morphology of the *Oocystis* cells did not change significantly in the presence of BPA (Fig. S2(b)). The maximal carbon capture rate of the *Oocystis* strain was 0.16 g/(L·d) which was much higher than that of the *Chlorella* strain (0.06 g/(L·d)). The *Oocystis* strain still maintained a good growth state under the prolonged stress of BPA, which was consistent with a relatively high tolerance to BPA and ultra-long growth cycle of the *Oocystis* strain, indicating the high potential of the *Oocystis* for long-term biological removal of BPA. Bacteria were widely used for BPA degradation. Ten strains of BPA-degrading bacteria isolated from desert soil could remove 36%–97% of BPA (Louati et al., 2019). *Oocystis* showed advantages including low environmental requirements, high removal rate, and low toxicity of by-products compared with bacterial degradation (Eltoukhy et al., 2020).

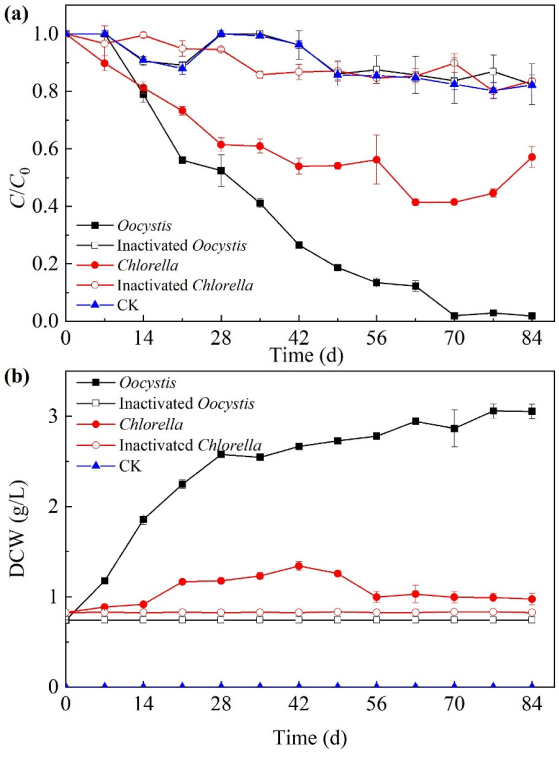

Fig. 1 Removal kinetics of BPA using *Oocystis* sp. YTLJ-NAPE-RC3 (a) and effects of BPA on DCW (b). (C_0 = 1000 μg/L, 20 °C).

3.2 Effects of initial concentration and temperature on the removal of BPA

The removal rate by the *Oocystis* strain increased with increasing BPA concentration (Fig. 2). The maximal removal rate increased from 4.40 to 29.80 μg/(L·d) when the BPA concentration increased from 100 to 2000 μg/L. On the other hand, high concentrations of BPA had an irreversible toxic effect on the *Chlorella*. The *Chlorella* could degrade BPA efficiently only at relatively low concentrations. The maximal removal rate by *Chlorella* increased from 2.23 to 23.08 μg/(L·d) when the concentration increased from 100 to 1000 μg/L while the maximal removal rate dropped to 15.63 μg/(L·d) when the BPA concentration increased to 2000 μg/L. Both the DCW (Fig. 2(b)) and BPA removal rate by *Oocystis* treatment were not affected under conditions of high BPA concentration, indicating the high removal potential of BPA using *Oocystis* sp. YTLJ-NAPE-RC3. Interestingly, the low concentration of BPA promoted the growth of *Oocystis*. This might be ascribed to the fact that BPA which was known as environmental hormone at low concentrations might serve as growth promoters for *Oocystis*. Similar phenomenon was found in a study of ethinyl estradiol (EE2) on *Microcystis aeruginosa* (Ma et al., 2023). Meanwhile, BPA did not have growth promotion but inhibition effect on the *Chlorella* control.

The most suitable temperature for BPA removal by *Oocystis* was 20 °C with a removal efficiency of 98.1% and a DCW of 3.35 g/L (Fig. 2). The removal efficiency of BPA dropped to 68.5% at 10 °C and 48.5% at 30 °C while the DCW dropped to 2.23 g/L at 10 °C and to 1.77 g/L at 30 °C. In terms of DCW, *Oocystis* is a genus that does not like high temperatures to grow rapidly at 20 °C and slowly at 30 °C or 10 °C. Compared with *Chlorella*, the *Oocystis* strain was more advantageous in BPA removal and carbon capture under both suitable and unfavorable temperatures.

3.3 Effects of inoculum level and pH on the removal of BPA

There was no significant difference in the inoculum level for the removal of BPA by the microalgae (p >

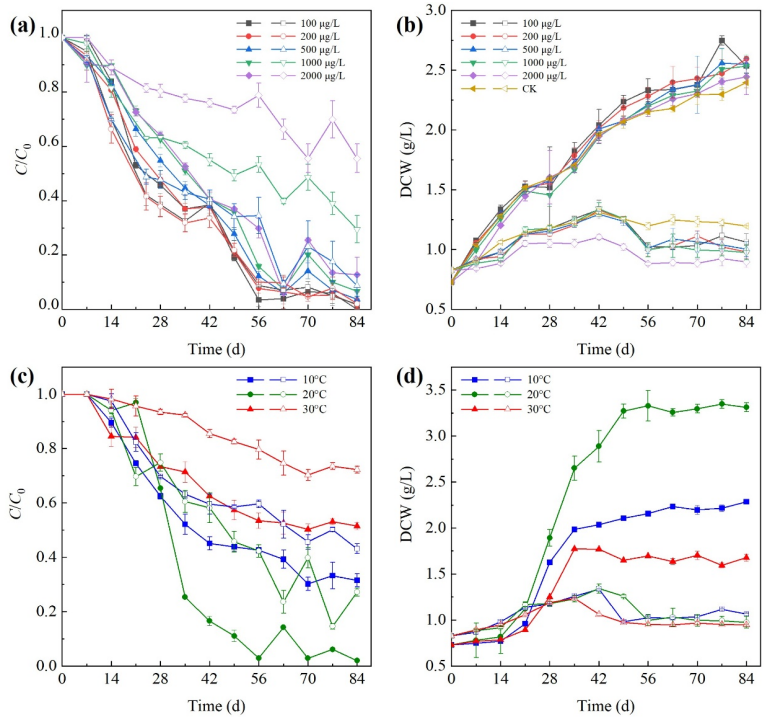

Fig. 2 Effects of (a, b) initial concentration and (c, d) temperature on the removal of BPA. (solid for *Oocystis*, hollow for *Chlorella*).

0.05) (Fig. 3). The BPA removal rates were 97.0%, 98.1%, 96.8%, and 97.2% with inoculum amounts of 1%, 2%, 3%, and 5% (v/v), respectively. The removal of BPA by the *Oocystis* strain showed a consistent trend in different pH regimes (Fig. 3). The BPA removal efficiency at pH 5.0 reached 95.84% on day 42 with a degradation rate as high as 3.78 μg/(L·d) from day 7 to day 28, coinciding with logarithmic growth phase of the microalgae. The *Oocystis* strain also maintained a good ability to remove BPA under alkaline conditions with BPA removal rates of 96.5% and 96.4% at pH 9.0 and 10.0, respectively. Previous studies reported that the growth of *Oocystis* was strongly influenced by pH with significant inhibition at pH 6.0 while microalgal growth densities were essentially the same under alkaline pH (Wei et al., 2022). This encouraging result showed that the *Oocystis* strain was more adaptable than *Chlorella* to pH and varying environmental conditions.

3.4 Effects of light intensity, salinity and carbon source on the removal of BPA

The BPA removal rate of the high/medium light experimental series was 85.4%/98.1% while that of the dark treatment group was only 8.1% (Fig. 4(a)), indicating that photosynthesis and the resulting autotrophic growth were essential for the removal of BPA by *Oocystis*. Indeed, strong light favored microalgae growth whereas dark treatment made growth slow. Light intensity affects the growth of microalgae by influencing the formation of fatty acids. Moreover, many microalgae are dependent on chemoenergetic heterotrophic growth in the absence of light energy so that they are unable to photosynthesize or proliferate under dark conditions (Perez-Garcia et al., 2011; Nzayisenga et al., 2020).

The removal of BPA showed a positive correlation with salinity since the final removal rates were 76.6%, 90.6%, and 96.9% at salinity of 10‰, 20‰ and 30‰, respectively (Fig. 4(c)). The growth of the *Oocystis* strain had the similar trend. Three carbon sources including glucose, sodium acetate and sodium bicarbonate were selected to investigate the effect of organic carbon sources on the removal of BPA by the *Oocystis* strain and the possible mixotrophic metabolism of these microalgae. The results showed that glucose and sodium acetate inhibited BPA removal with respective removal efficiencies of 72.1% and 88.9% while the treatment with sodium bicarbonate had a removal efficiency of 96.6% which were comparable to that under autotrophic growth with CO_2 (Fig. 4(e)). The glucose addition treatment resulted in a higher specific growth rate than the blank control (without additional carbon source) during 14–28 d, suggesting

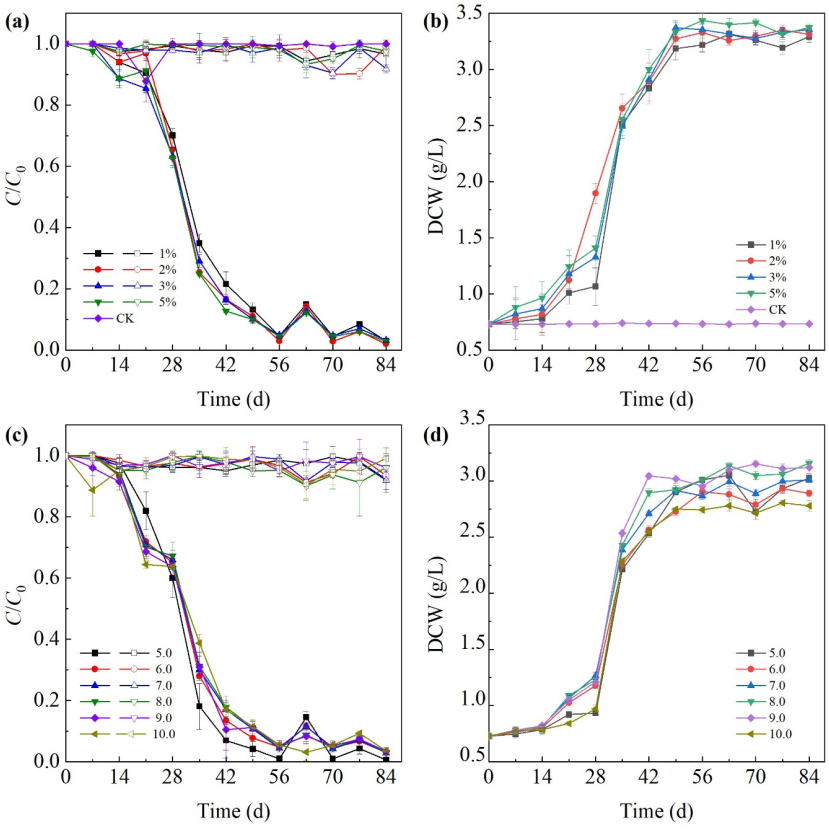

Fig. 3 Effects of inoculation amount (a, b) and pH (c, d) on the removal of BPA. (solid for *Oocystis*, hollow for inactivated *Oocystis*).

that the glucose addition could promote the heterotrophic growth of *Oocystis*. Most of microalgae could use the sugar metabolic pathway to produce acetyl coenzyme A which took part in the tricarboxylic acid cycle (Ruiz et al., 2022).

3.5 Antioxidation response mechanisms of the *Oocystis* strain to BPA

Microalgae cells trigger a variety of self-protective mechanisms such as increasing the levels of various antioxidant enzymes to adapt and counteract the stressful effects of toxic substances (Drira et al., 2021). SOD enzyme activities (Fig. 5) of *Oocystis* sp. YTLJ-NAPE-RC3 in all experimental series for the BPA treatments were much higher than those of *Chlorella*, indicating very strong antioxidant protection of the *Oocystis* cells during the BPA removal process. Compared with the blank control (no BPA), POD and CAT enzyme activities increased with the increase of BPA concentration. The same phenomenon were observed in previous studies (Fu et al., 2023). Meanwhile, the POD activities of the *Oocystis* strain in all BPA treatments were much higher than those of *Chlorella*, confirming the strong antioxidant protection of the *Oocystis* cells during the BPA removal process. The increase in the POD activity also suggested that POD could be involved in the degradation of BPA. The POD was proved as the essential enzymes for the biodegradation of many pollutants (Wu et al., 2022). The MDA which is an indicator of cell peroxidation (Valavanidis et al., 2006) content increased from 0.16 to 0.86 nmol/mgprot when the concentration of BPA increased from 0.1 to 10 mg/L, illustrating that high concentration of BPA could activated the nonenzymatic oxidative stress system of the *Oocystis* cells and led to the damage.

3.6 Transcriptomic analysis of *Oocystis* in the presence and absence of BPA

Transcriptomic analyses between the control (no BPA) and BPA (10 mg/L) treatment with *Oocystis* revealed 21693 differentially expressed genes (DEGs) including 2950 up-regulated DEGs (red points) and 18743 down-regulated DEGs (blue points) (Fig. 6(a)). Figure 6(b) was a heatmap of differentially expressed gene clustering. The trend of unigene expression change

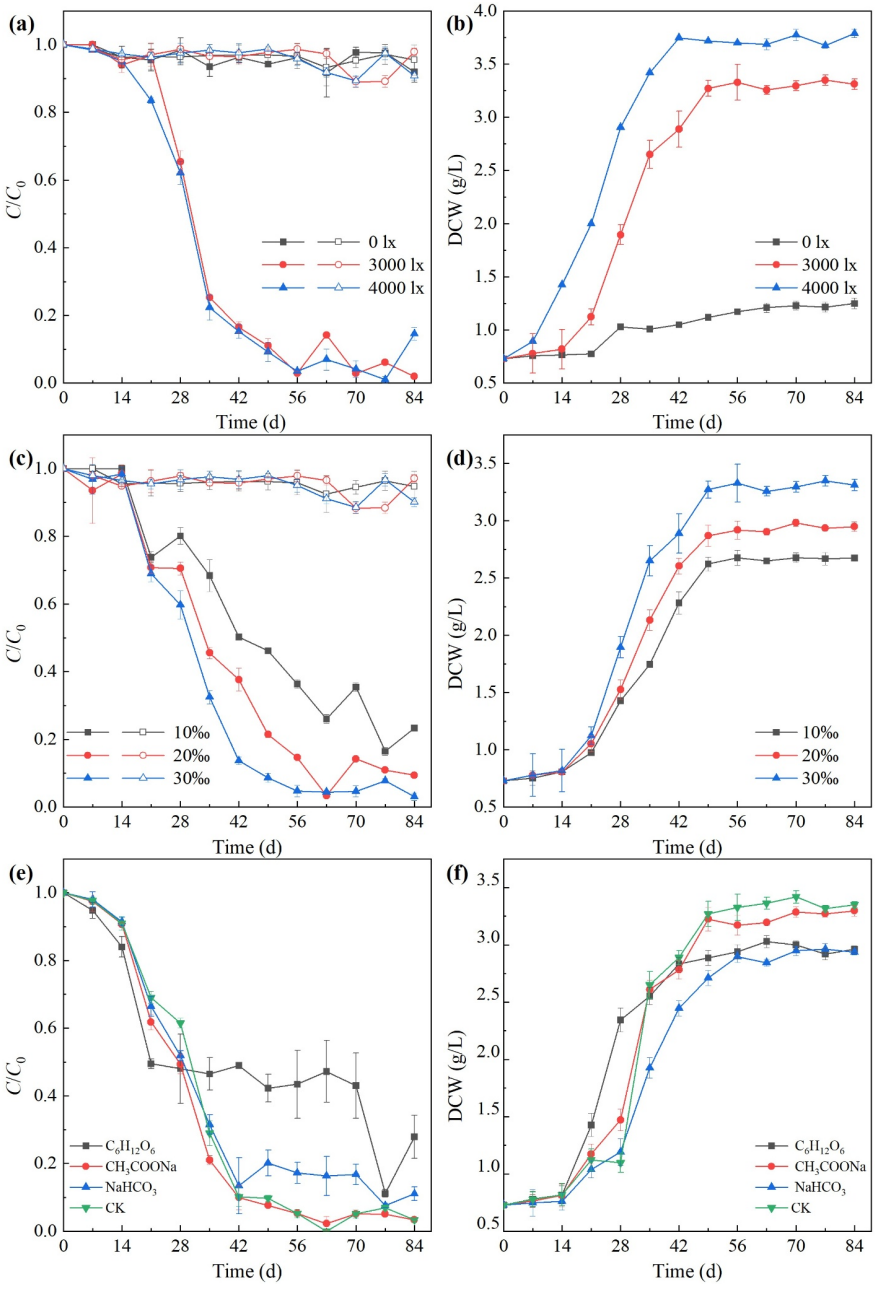

Fig. 4 Effects of light intensity (a, b), salinity (c, d) and additional carbon source (e, f) on the removal of BPA (solid for *Oocystis*, hollow for inactivated *Oocystis*).

within the group was close. The clustering between the two groups was reasonable while the differences in gene expression were significant. Several GO terms were enriched under BPA exposure in the categories of biological processes (metabolic processes and cellular processes), cellular components (cell part, membrane and organelle), and molecular functions (binding and catalytic activity) to reveal gene and protein functions (Fig. 6(c)). The significantly enriched terms were further analyzed to explore the function of expressed genes. Photoreceptor (GO:0009881) converted light energy into bioelectrical or chemical signals, which might significantly contribute to photosynthesis. Regulation of response to stimulus (GO:0048583) was related to the antioxidant system. ATP biosynthetic process (GO:0006754) and organic anion transmembrane transporter activity (GO:0008514) were pivotal for energy metabolism, biochemical reactions

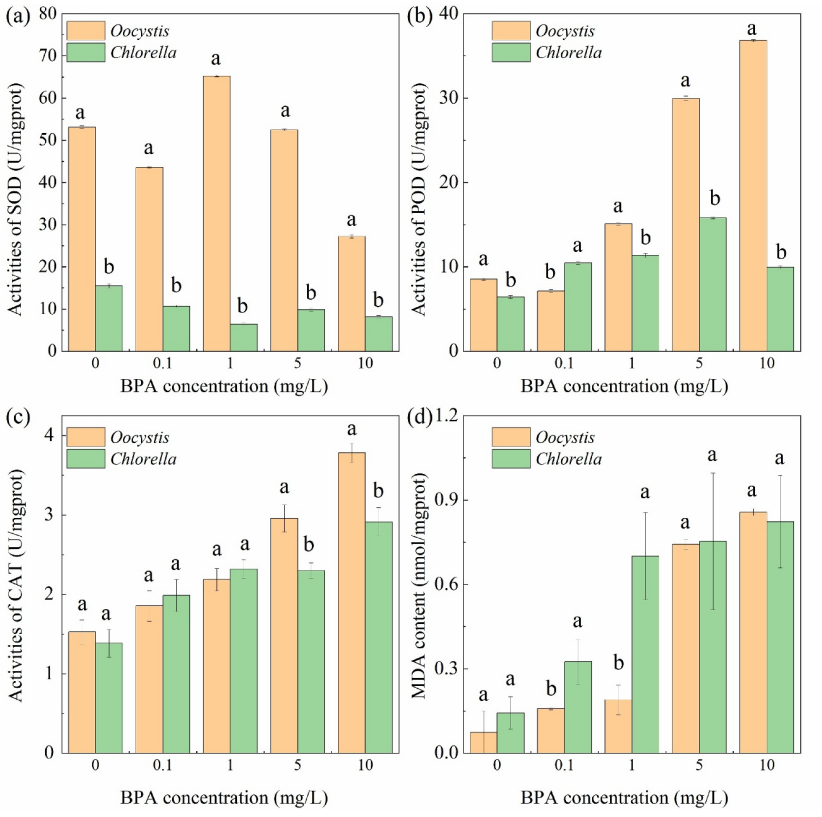

Fig. 5 Activity of SOD (a), POD (b), and CAT (c) enzymes as well as the MDA (d) content in microalgae at different BPA concentrations.

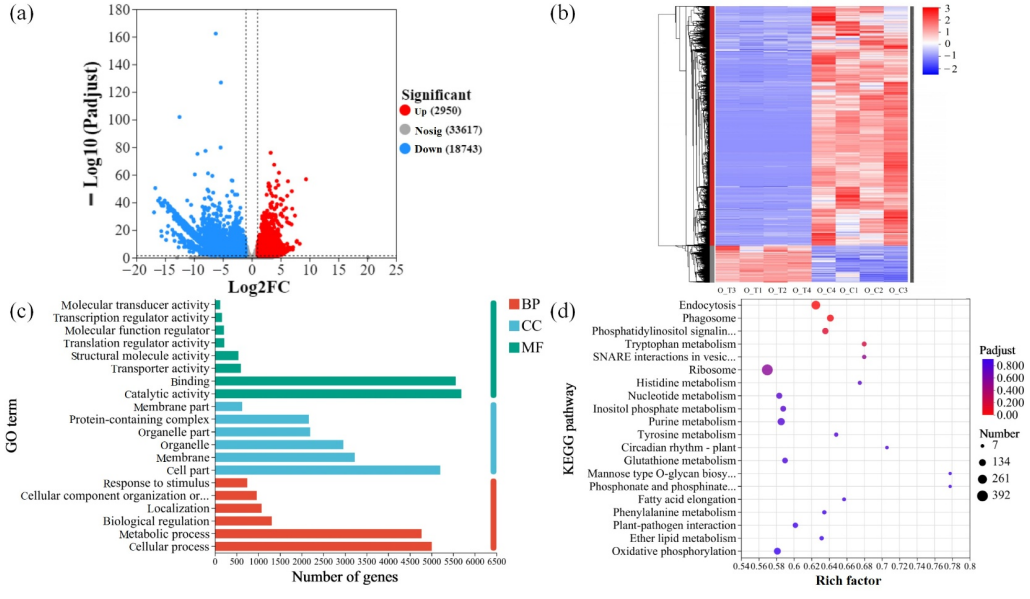

Fig. 6 Differentially expression of genes in BPA treatment and control groups. Volcanic map for DEGs (a). Hierarchical cluster analysis of DEGs (b) (O_T1-O_T4 for control group, O_C1-O_C4 for BPA treatment group). GO enrichment of DEGs (c). KEGG enrichment of DEGs (d).

and cell activation. These functional processes enabled *Oocystis* to adopt adaptive strategies for mitigating BPA toxicity and promoting algal cell growth through self-adaptive regulatory mechanisms (Ha et al., 2025). The KEGG analysis suggested that BPA mainly affected the photosynthesis of the *Oocystis* strain (Fig. 6(d)). Endoplasmic phagocytosis in the endoplasmic reticulum had more annotated DEGs than other pathways. Significance analysis revealed that the most significantly enriched KEGG entry was endoplasmic phagocytosis while other pathways such as those involved in phagolysosomes and tryptophan metabolism were also significantly enriched. The enrichment of tryptophan metabolism which was essential for the synthesis of auxin, confirming that BPA could serve as growth promoters for *Oocystis*. Meanwhile, the enrichment of the binding and metabolism, glycan synthesis and metabolism demonstrated that BPA might be also removed through the glycosylation process. Previous investigation showed that the contribution of BPA conjugation such as glycosylation could exceed 50% (Liao and Kannan, 2012).

Differential genes were significantly enriched ($p < 0.05$) in the glutathione metabolism-related pathway (Table S3). Among these genes, the expression levels of POD-related genes changed significantly after BPA treatment. The up-regulated POD genes were glutathione related genes, suggesting that glutathione POD involved in the BPA biodegradation. Glutathione is a small molecule thiol ubiquitous in cells that plays a major role in maintaining intracellular redox homeostasis and regulating signaling pathways increased by oxidative stress (Haddad and Harb, 2005). Glutathione could effectively scavenge reactive oxygen species from microalgal metabolism and environmental stresses to help plants resist external stresses (May et al., 1998). Differential genes were also enriched in pathways related to glutathione metabolism after BPA treatment. The expression of genes related to glutathione metabolism (TRINITY_DN6511_c1_g2 and TRINITY_DN6511_c1_g2) was up-regulated. The up-regulation of these genes facilitated the maintenance of intracellular glutathione synthesis and reduction, which helped algae effectively remove reactive oxygen species and improve the resistance of microalgae to oxidative stress. Previous study also found that the submerged macrophyte *Ceratophyllum demersum* L. could resist the environmental stress of BPA by increasing glutathione synthesis (Zhang et al., 2017). As for SOD-related genes, three genes were up-regulated and six genes were down-regulated after BPA treatment. The enrichment of the CYP450 related genes was not significant, indicating that the CYP450 was not engaged in the biodegradation of BPA.

Photosynthesis provides energy for growth and reproduction of microalgae and photosynthetic pigments play an important role (Herrera and Roca, 2023). The content of total chlorophyll was inversely correlated with BPA concentration (Fig. 7(a)), indicating that high concentrations of BPA resulted in low concentrations of photosynthetic pigments. The contents of chlorophyll *a*, chlorophyll *b*, and carotenoids of the *Chlorella* control were much lower than those of the *Oocystis* treatment when BPA concentration exceeded 1 mg/L, confirming that the *Oocystis* strain was more tolerant to BPA than the *Chlorella*. The *PsbB* gene which encoded a product constituent of CP47 subunit of the photosystem II (PSII) was down-regulated under the exposure of BPA (Fig. 7(b)), which explained why the chlorophyll in the experimental group decreased (Barber et al., 1997). The cytochrome b_6/f complex *PetB* and *PetC* which contributed to the photosynthetic pigment were also down-regulated when *Oocystis* was used for BPA removal (Zhang et al., 2023c). The number of the up-regulated was much higher than that of the down-regulated photosynthesis functional genes, confirming the high tolerance of the *Oocystis* strain for BPA pollution. The number of photosynthetic functional genes was up-regulated despite photosynthetic pigment content decreased, suggesting that *Oocystis* tried to maintain basic physiological functions by up-regulating photosynthetic genes to compensate for other metabolic pathways impaired by BPA stress. *Oocystis* tried to find new survival strategies by adjusting gene expression. For example, the *PsbQ* proteins were extrinsic subunits of the PSII super-complex, which were found in green plants including higher plants and green algae. *PsbQ*, *PsbP*, and *PsbW* had specific roles in coordinating the activity of the donor and acceptor sides of PSII as well as stabilizing the active form of the PSII-light-harvesting complex II (LHCII) (Ifuku et al., 2011). Similarly, *PsbZ* was up-regulated to stabilize the PSII (Swiatek et al., 2001). *PsbO* protein was an important peripheral protein in PSII, which played a key role in photosynthetic oxygen release, stabilization of manganese clusters, water oxidative cleavage, and electron transfer. *PsbO* was essential for maintaining the structural and functional integrity of PSII (Popelkova and Yocum, 2011).

3.7 Biotransformation pathway of BPA using the *Oocystis* strain

Five intermediate metabolites were detected by HPLC-

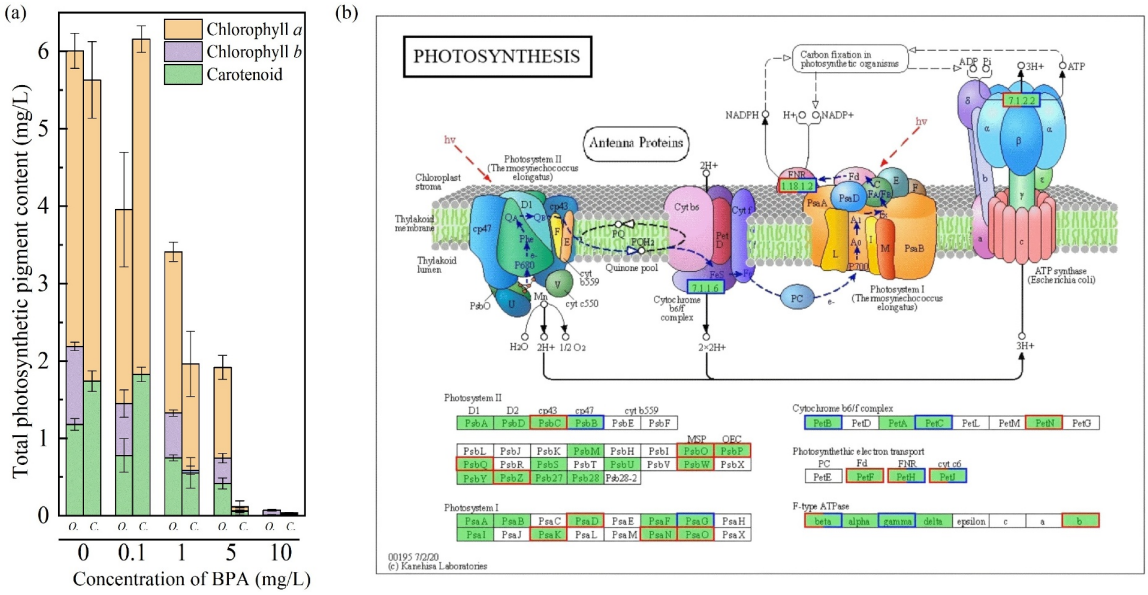

Fig. 7 Photosynthetic pigment content (a) of microalgae at different BPA concentrations (*O.* for *Oocystis*, *C.* for *Chlorella*) and the influence of BPA on the metabolic pathways of photosynthesis of the *Oocystis* (b) (The green boxes indicated the genes annotated in this project. The red borders indicated that the gene was up-regulated while the blue borders indicated that the gene was down-regulated. The combination of red and blue borders indicated that the gene was both up-regulated and down-regulated.).

QTOF-MS in negative ion mode (Fig. S3). These intermediate metabolites were identified as benzoquinone (m/z 107), *p*-isopropyl phenol radicals (m/z 134), phenol (m/z 93), 4-(*tert*-butyl)-2-(2-(4-hydroxyphenyl) propan-2-yl) phenol (m/z 283), and 4-4 '-dihydroxybenzophenone (m/z 213). The metabolic pathways of BPA were postulated (Fig. 8(a)). In pathway 1, BPA was hydroxylated to form 4-4'-methane dimethylene diester, which was subsequently converted to benzoquinone (Li et al., 2019). Based on previous investigations, the pathway 2 might include the attack of the carbon double bond between the two benzene rings of BPA to undergo isopropenyl cleavage to produce *p*-isopropyl phenol radical and phenol. The isopropyl phenol radical is capable of attacking the neighboring hydroxyl group of the benzene ring of BPA to produce 4,4'-(4-hydroxy-1,3-phenylene)bis (propane-2,2-diyl)bisphenol. This intermediate is cleaved to form phenol and 4-(*tert*-butyl)-2-(2-(4-hydroxyphenyl)propan-2-yl)phenol, where the latter can undergo further scission to form phenol (Lin et al., 2020). Transcriptome analysis showed that genes related with glutathione peroxidase were up-regulated in *Oocystis* in the presence of BPA, suggesting that peroxidase played an important role in BPA degradation. Previous study showed that peroxidase could convert BPA to 4-isopropenylphenol through desaturation (Zhang et al., 2017). In pathway 3, BPA was converted to 4-4'-dihydroxybenzophenone by demethylation, and subsequently broken down to 4-hydroxyacetophenone. Eventually, the benzene ring might be mineralized into the final products CO_2 and H_2O (Diao et al., 2020). Besides, the conjugation process might be another essential process for BPA removal based on the transcriptomic analyses. Previous investigations showed that conjugation such as glycosylation was an important transformation pathway for the BPA in plant and animals (Liao and Kannan, 2012; Lu et al., 2022).

The developmental toxicity and bioaccumulation factor of BPA and the corresponding intermediates were assessed through Toxicity Estimation Software (TEST) according to a previous study (Cai et al., 2019). The postulated biodegradation products of BPA showed relatively lower values of developmental toxicity and bioaccumulation factor (Fig. 8(b)), suggesting that the degradation of BPA was also accompanied by the detoxification effect.

3.8 BPA removal and carbon capture using *Oocystis* in the bio-pilot scale system

In the bio-pilot scale tailwater treatment system, the *Oocystis* strain still maintained high BPA removal efficiency and carbon capture capacity. BPA was entirely eliminated within 14 d and the carbon capture

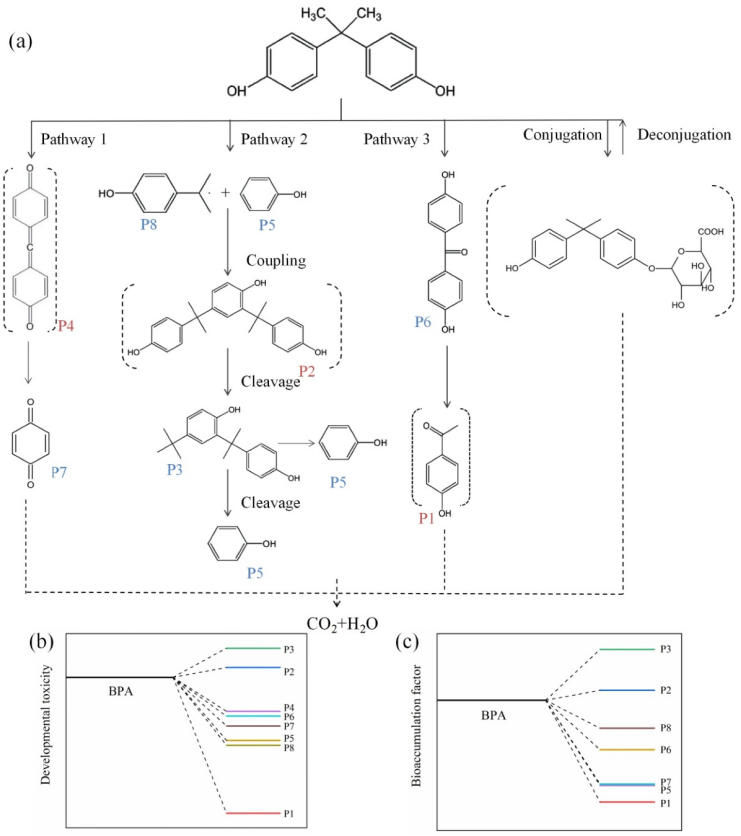

Fig. 8 Degradation pathway (a), theoretical calculated developmental toxicity (b), and bioaccumulation factor (c) of BPA and their degradation intermediates.

rate could reach 0.2 g/(L·d). The *Oocystis* strain also demonstrated the ability to remove nitrogen and phosphorus from aquaculture tailwater. The removal efficiency of ammonia nitrogen was 90.9% while that of the active phosphate was up to 88.5%.

3.9 The distinctions in BPA degradation characteristics between the *Oocystis* and other microalgae

Through comparison with existing literature (Table S4), our study demonstrated that the *Oocystis* achieved a 100% removal efficiency of BPA, outperforming most reported microalgae in BPA elimination. The optimized culture conditions for BPA removal by *Oocystis* sp. were as follows: temperature was 20 °C, inoculum was 2%, pH was 8.0, and salinity was 30‰. Notably, the growth duration of the *Oocystis* strain exceeded 84 d, which was far beyond the other microalgae used for BPA removal. The primary pathway for BPA removal by *Oocystis* was identified as biodegradation while that of many other microalgae was biosorption.

4 Conclusions

This study demonstrated the breakthrough progress on using microalgae *Oocystis* sp. YTLJ-NAPE-RC3 for highly efficient simultaneous BPA removal and carbon capture in seawater system. Compared with *Chlorella*, the removal rate of BPA was doubled while the carbon capture rate was almost tripled using the novel *Oocystis* strain. The *Oocystis* strain demonstrated ultra-long growth cycle and the relatively high tolerance to BPA. The temperature, salinity, and initial concentration of BPA could influence the removal of BPA using *Oocystis* while other factors such as pH, inoculum amount, and light intensity had weak effects. The relatively high SOD and POD activities of the *Oocystis* strain indicated its extremely strong antioxidant self-protection and the involvement of POD during BPA removal. Transcriptome analysis showed that BPA mainly affected the photosynthesis-related genes of the *Oocystis* strain and demonstrated the engagement of glutathione POD during the BPA biodegradation. BPA could serve as growth promoter for *Oocystis* during the removal process with the relatively low concentration,

which subsequently enhanced the growth and carbon capture. Finally, BPA could be removed by the *Oocystis* strain through hydroxylation, demethylation, and conjugation. These findings provide new insights on the potential of *Oocystis* to efficiently control the emerging micropollutant and carbon capture. The *Oocystis* might also have good potential in the remediation of other pollutants in the future. The application of *Oocystis* is expected to achieve sustainability from laboratory scale to practical application.

Conflict of Interests Jian Lu is an Editorial board member of *Frontiers of Environmental Science & Engineering*. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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