water

Review

Influencing Factors for the Growth of *Cladophora* and Its Cell Damage and Destruction Mechanism: Implication for Prevention and Treatment

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Abstract: *Cladophora* is commonly found in marine and freshwater around the globe and provides productivity for littoral zone microorganisms and invertebrates. The eutrophication of the water body has led to the abnormal proliferation of *Cladophora* in some water, often in river coast channel outbreaks. Even under the nutritional deficiency systems, such as the central trunk canal of the South-to-North Water Diversion in China, *Cladophora*'s blooms affect water quality and seriously jeopardize human health. Thus, the structural characteristics of *Cladophora* cells and spores, the factors affecting the growth of *Cladophora* cells, and the mechanisms of damage and destruction of *Cladophora* cells and spores were investigated. *Cladophora* cells are cylindrical with very thick cell walls. The inner layer of the spore wall is a thin membrane which contains the nucleus of the spore. The growth and spreading of *Cladophora* cells are affected by various environmental factors such as light, temperature, water depth, water level, nutrient salts, pH, etc. Some physical treatment measures, such as ultrasounds, would destroy the cell walls and membranes of *Cladophora* by its high-intensity mechanical action. Chemicals and aquatic plant measures can destroy *Cladophora* cells' photosynthesis system, antioxidant enzyme systems, proteins, and ultrastructure. Based on the mechanisms for these cell damage and destruction, a combination of measures that are likely to inhibit the growth of *Cladophora* cells effectively was suggested. Furthermore, the damaged cells of *Cladophora* could provide some environmental benefits. Aggregated results could provide a scientific basis for further research on the control of blooms of *Cladophora* or the reuse of *Cladophora* cells as a natural resource.

Keywords: *Cladophora*; cell; growth; damage and destruction; mechanism

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1. Introduction

Cladophora is *Chlorophyceae*, a member of the family of *Cladophoraceae*, which is a filamentous, green, branching algae [1]. *Cladophora* belongs to the higher algae and contains chlorophyll identical to that of higher plants. The water environment of *Cladophora* is well adapted to low CO_2 and can rapidly absorb CO_3^{2-} as a supplementary carbon source when there is insufficient CO_2 in the water [2]. Thus, *Cladophora* is more able to adapt to low CO_2 environments than algae in general. *Cladophora* is ubiquitous in marine and freshwater worldwide, as it provides productivity for littoral zone microorganisms and invertebrates [3]. *Cladophora* can grow exceptionally well in eutrophic waters and has applications in a number of industries [4]. Wastewater can be purified with the use of

Cladophora, which is simpler and less costly in terms of process compared to traditional treatment methods [5]. The biofilm area of *Cladophora* is large, and studies have shown that it is effective in intercepting and adsorbing microplastics [6]. The effect of *Cladophora* in removing N and P from eutrophic water is significantly higher than that of Diatoms and Cyanobacteria [7]. *Cladophora* also has good adsorption capacity of Pb, Cd, and As in the water body [8,9]. Therefore, the moderate growth of *Cladophora* would have a positive effect on water's consumption of nutrient salts, purifying water quality and maintaining the balance and stability of the water ecosystem. However, excessive proliferation of *Cladophora* can inhibit the growth of other aquatic organisms, produce harmful substances such as H_2S, and damage water quality. This leads to negative impacts on water ecosystems and water quality safety [10].

Currently, abnormal algal accretion and algal bloom outbreaks are environmental problems that are extremely difficult to solve. Due to its abnormal proliferation, it has led to significant threats to the availability of water bodies, biodiversity, and landscape [11]. *Cladophora* has become one of the classic algae species for algal bloom outbreaks due to its strong reproduction ability and fast growth cycle. The proliferation of Cladophora has been reported in many rivers, lakes, and other water bodies in different regions of the world, such as Lake Baikal (East Siberia), Laurentian Great Lakes (USA), Lake Budworth (UK), and Qinghai Lake (China) [12–15]. It was found that a large number of *Cladophora* grow in Qinghai Lake, China, and most of the areas with significant *Cladophora* biomass are submerged grasslands (>500 g/m^2) [12]. In recent years, *Cladophora* has been prone to bloom in August. Their unique food chain is simpler than that of other lakes at lower elevations, so outbreaks of *Cladophora* can wreak havoc on their water quality [14]. Transitional proliferation of *Cladophora* has gradually become a widespread global problem. With the intensification of eutrophication in global water bodies, *Cladophora* has appeared in different scales of outbreaks in coastal zones, which may endanger the growth of fish fry and cause severe environmental problems. At the same time, the abnormal increase in the value of *Cladophora* also affects the recovery of submerged plants in the environmental restoration process of some lakes. Compared with eutrophic water bodies, the problem of abnormal proliferation of *Cladophora* is currently occurring even in some low-nutrient water bodies. For example, under low nutrient conditions (TN < 1.50 mg/L, TP < 0.026 mg/L) in the central trunk canal of the South-to-North Water Diversion in China [16], abnormal proliferation of *Cladophora* still existed for some years. This led to clogging of the filter media layer, affecting the regular operation of the filtration system [17]. Due to the large size of *Cladophora* cells, it is easy to block the filter device. In addition, *Cladophora* cells attach siliceous cell walls to hard shells. These create easy-to-adsorb sticky substances that are not easily destroyed by disinfectants. These make water quality treatment difficult and increase costs [18].

The *Cladophora* not only reproduce rapidly but are also very difficult to control. Patrick et al. [19] reported a series of biological control measures for freshwater *Cladophora* at an early stage but did not find any animals feeding on *Cladophora*. Some studies have shown that other chemical methods, such as $CuSO_4$, can also inhibit the growth of *Cladophora*. However, it can have toxic effects if added in excess [20]. In general, the more widely used means of algae removal have shortcomings, such as low efficiency, maintenance difficulties, and secondary pollution. At the same time, there are few reports on the methods to effectively inhibit the propagation of *Cladophora* in the actual water environment. Factors affecting the growth and propagation of *Cladophora* cells, as well as the mechanism of damage to their cells by means of prevention and control, are the basis for scientific prevention and control of the abnormal proliferation of *Cladophora* in the aquatic environment and even for the recycling and utilization of *Cladophora* cell resources. Therefore, the present study is intended to summarize the factors affecting the cell growth of *Cladophora* based on a large number of reports in the literature. Based on the structural characteristics of the cells of *Cladophora* and the damage mechanism of the cells during the prevention and control of algal species. This study will analyze the mechanism of the destruction of the cellular structure of *Cladophora* through physical, chemical, and biological methods. Ultimately, theoretical methods for the integrated control and utilization of *Cladophora* cells will be proposed. Acquiring these results is favorable for the development of devices and engineering applications in the future.

2. Characterization of the Cell Structure and the Process of Matter-Energy Cycling in *Cladophora*

Cladophora larvae are embedded and float when they grow. The cells are long and cylindrical, with a thick cell wall [21], as shown in Figure 1. The cells have a large central vacuole, and the pigment bodies are granular during the spore period of the *Cladophora* and reticulate when the cell matures [21]. When mature, the cell can be dispersed into multiple protein nuclei and nuclei [22]. *Cladophora* contain chlorophyll a (Chla) and chlorophyll b (Chlb). The cell wall is layered with a cuticle that contains 70% protein. It is often epiphytic with many algae [23]. The basal cells form pseudoradical branches that are 25–35 µm wide. They are 5–8 times as long as wide [22]. *Cladophora* grows by apical or intermediate cell division and fixes by basal cells, pseudoroots, or fixators [22]. *Cladophora* cell division is caused by the cytoplasm producing ring-like constriction grooves and septa formed by the deposition of cell wall material in the grooves, separating the cell in two. The cytoplasm does not divide at the same time [24].

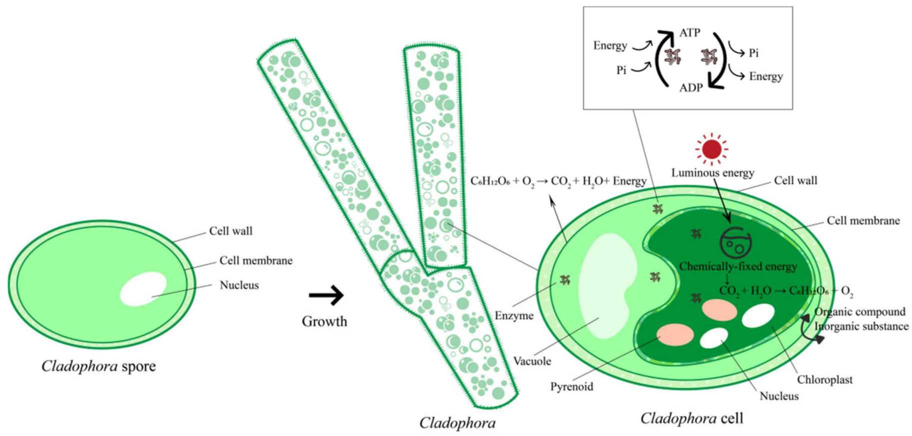

Figure 1. Diagram of spore and cell structure and the process of matter-energy cycling in *Cladophora*.

The *Cladophora* can reproduce asexually or produce spores [25]. The shape and size of *Cladophora* spores vary from short and thick rod-shaped, elongated, and spindle-shaped, with sizes ranging from 2 to 20 µm [21]. The surface of the spore wall has short and dense setae, which are essential structures for the spores to float, move, and reproduce in the water. The inner layer of the spore wall is a thin membrane that contains the nucleus of the spore. The outer layer of the spore wall is a hard shell with many tiny holes on the surface of the shell, which allow for the exchange of substances inside and outside the spore wall [26].

Compared with other planktonic algal cells and aquatic plant cells, the *Cladophora* cell has a unique morphology and structure. As mentioned earlier, the *Cladophora* cells are cylindrical, which differs from most planktonic algal cells and aquatic plant cells. *Cladophora* cells form elongated rod-like projections at the edge of the cell that are encapsulated by tiny vacuoles that contain specialized enzymes that may be used to break down organic matter [6]. In addition, the chloroplasts of the *Cladophora* cells also exhibit a unique structure compared to other planktonic algal cells. In chloroplasts, *Cladophora* cells contain a large number of vacuoles, and the membranes of these vacuoles are rich in transmembrane proteins, which may be one of the essential reasons why chloroplasts maintain efficient photosynthesis [21]. Cyanobacteria do not have organelles such as chloroplast, mitochondrion, centrosome, endoplasmic reticulum, and vacuole [27]. However, Cyanobacteria contain

Chla and phycocyanin, which can photosynthesize with the help of enzymes and pigments in the cytoplasm [28].

Cladophora cells use photosynthesis and respiration for material and energy cycling (Figure 1). *Cladophora* cells absorb light energy and convert it into chemical energy. *Cladophora* cells can photosynthesize and synthesize organic matter, which is stored inside the cell [2]. At the same time, photosynthesis produces oxygen, which is taken up by the algal cells and replenishes the oxygen needed. *Cladophora* also converts organic substances, such as glucose, into energy through aerobic respiration, which powers the cells to maintain life activities. In addition, there are different types of enzymes that are involved in various metabolic processes within the cell, which break down organic substances into smaller molecules, releasing energy to power the cell's life activities [21]. Inside the cells of the *Cladophora*, organic and inorganic substances are transferred through organelles in the cytoplasm and the cell membrane, through which CO_2 is expelled from the cell. The *Cladophora* is very adaptable to low CO_2. When there is insufficient CO_2 in the water, they can utilize HCO_3^- as a source of carbon very quickly, unlike other algae that need a period of time to adapt. *Cladophora* cells can use HCO_3^- for the photosynthesis of carbonic anhydrase. Through metabolic activities such as photosynthesis, they consume HCO_3^- in the water and deposit $CaCO_3$ [2].

3. Factors Influencing Cell Growth and Dissemination and Critical Processes in *Cladophora*

The growth and propagation of *Cladophora* cells can be influenced and regulated by a variety of environmental factors. The conceptual diagram of the factors and processes affecting the propagation and growth of *Cladophora* cells in the actual aquatic environment is shown in Figure 2. The environmental factors related to the growth of *Cladophora* cells are generally light, temperature, hydrodynamics, water depth, water level, nutrient salts, and pH.

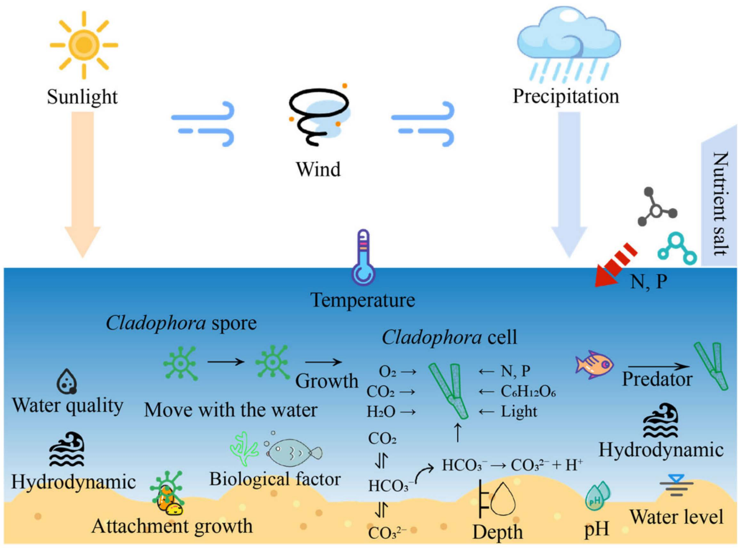

Figure 2. Factors affecting the growth and propagation of *Cladophora* cells and their processes.

Light is an important environmental factor influencing the distribution of *Cladophora* communities over time and space. Sometimes, there are interactions between environmental factors [29]. When the light intensity reaches saturation point, the photosynthetic rate decreases or even stops, and photoinhibition occurs [30]. According to Graham et al. [31], the light saturation point of *Cladophora* was in the range of 15.4–30.8 $\mu mol_{photons}/m^2/s$ under different temperature conditions. *Cladophora* is very sensitive to light and prefers to stay in more adequate light conditions [32]. However, there are algae that do not like bright light; for example, *Rhodophyta* reproduces faster under moderate light conditions [33].

Seasonal changes in the biomass or abundance of *Cladophora* tend to be a response to temperature. Low-temperature conditions in winter and spring inhibit the growth of *Cladophora*, which requires a minimum water temperature of about 5 °C for growth, and studies have shown that *Cladophora* gradually dies when the water temperature exceeds 23.5 °C in summer [34]. According to Stewart and Lowe [35], the optimal water temperature for growth of *Cladophora* ranges from 5–23 °C. The optimal temperature for growth of *Cladophora* differs significantly from that of planktonic algae. For example, *Cyanobacteria* grow at 28–35 °C, while *Diatoms* maximize their specific cell growth rate and significant physico-chemical content at 15–25 °C [31].

Changes in hydrodynamic conditions can lead to changes in water column material transport, affecting algal growth [36]. Water flow can enable the exchange of oxygen and carbon dioxide in the water environment with the atmosphere, which also helps to ensure the supply of nutrients. Water movement also affects the growth of *Cladophora* through stretching, dragging, and churning. Hydrodynamics also has an essential effect on the shedding of *Cladophora* cells. The speed and direction of water flow can directly affect the state and stability of *Cladophora* cells [37]. In the case of fast water currents, *Cladophora* cells face greater tensile forces and are easily dislodged by the current. Slow currents make the *Cladophora* cells more stable and allow for better attachment to the surface of the object. When the direction of water flow changes, the *Cladophora* cells need to re-adapt to the new flow environment, which may lead to cell detachment. It has been found that *Cladophora* collected from reservoirs have many branches, while those collected from flowing water, such as rivers, have fewer branches [22]. Whereas *Cladophora* usually grows in slower currents, planktonic algae can adapt to a variety of current conditions and can grow in faster currents [38]. There is also a relationship between *Cladophora* cell growth and water depth. Light intensity in nature also decreases with increasing water depth, mainly due to the influence of suspended solids in the water column, including plankton. It has been found that the biomass of *Cladophora* decreases with increasing water depth [39,40]. Water level is one of the critical factors determining the distribution, biomass, and population structure of aquatic plants, and moderate changes in water level would benefit the diversity of aquatic plant species [41]. Some studies have shown that in areas with water depths <1.0 m, sufficient sunlight can be allowed to penetrate to support *Cladophora* outbreaks [12].

Nutrients necessary for algae growth include N, P, Si, Fe, and other elements. Life processes such as photosynthesis, synthesis of organic compounds, and construction of tissue cells in *Cladophora* require the participation of various nutrient elements. Nutrient salt concentration affects physiological and biochemical conditions [42]. Phosphorus is the primary nutrient limiting the growth of *Cladophora* [35]. In eastern Lake Erie, mean concentrations of soluble phosphorus in the spring and summer growth periods of *Cladophora* ranged from 0.9 to 3.5 $\mu g\ L^{-1}$ [43]. An appropriate increase in pH favors photosynthesis and promotes the growth of *Cladophora*, but when the pH is too high, it is detrimental to the growth of *Cladophora* [44]. Alkaline water can easily absorb atmospheric CO_2 and promote photosynthesis of *Cladophora*. The main factors affecting the pH change of the reaction system are the photosynthesis and the respiration of *Cladophora*. Photosynthesis is stronger than respiration, CO_2 in the water is utilized, the acid-base equilibrium is disrupted, and the pH increases [45]. *Cladophora* utilizes HCO_3^- for photosynthesis; when HCO_3^- consumes H^+ to produce CO_2, the amount of H^+ decreases, the amount of OH^- increases, and the pH also increases. The predominant carbon form at pH 5 to 9 is HCO_3^-; at low pH, it is CO_2, and at high pH, it is CO_3^{2-} [46]. Tsutsui et al. showed that there was an interaction between salinity and pH and a highly significant effect on the growth of *Cladophora* [46].

The process of the spreading of *Cladophora* cells is also affected by a number of other factors, including temperature, light, water quality, hydrodynamics, and biological factors. Generally, water temperature between 15–30 °C is the optimal temperature for cell spreading of *Cladophora* [47]. Below 15 °C, cell spreading slows down. Water temperature levels above 30 °C lead to cell death. Cell spreading in *Cladophora* is accelerated under adequate light conditions and slowed down under inadequate light conditions [48]. Water quality also affects the cell spread of *Cladophora* [49]. Poor water quality and low levels of nutrients and oxygen can lead to limited growth and reproduction of *Cladophora*, thus affecting cell spread. Hydrodynamics is also an essential factor influencing the cell spread of *Cladophora*. Cell spreading of *Cladophora* is accelerated under faster water currents and slowed down under slower water currents [50]. The cellular spread of *Cladophora* can also be affected by other organisms. For example, some aquatic animals prey on *Cladophora*, thereby reducing their cellular spread [51].

4. Mechanisms of Cell Damage Destruction in *Cladophora*

Currently, common control methods for algae, including *Cladophora*, can be categorized into three main groups: physical, chemical, and biological. However, few studies have been reported on the prevention and control of *Cladophora* alone. The mechanism of cell damage and destruction is a critical scientific issue in the prevention and control of *Cladophora* and the reuse of cell fragmentation. It is essential for the research and growth of prevention and control technology and reuse means, but it has also been rarely reported. Therefore, this study will focus on physical, chemical, and biological effects and will combine this research with consideration of the characteristics of the cellular structure of the *Cladophora* and factors influencing the growth of *Cladophora*. In addition, we will analyze and explore the possible damage mechanism of *Cladophora* cells.

4.1. Mechanism of Cell Damage and Destruction of Cladophora under Physical Action

Physical methods mainly include traditional mechanical salvage, interception by interceptor poles, and hydrodynamic regulation. Some new technological methods, such as physical shading, ultrasound, micro-current, ultraviolet (UV), zeta potential, and many other methods, have been reported but are not widely used [52–54]. Due to the characteristics of vertical distribution and horizontal drift of *Cladophora*, which are directly affected by thermal stratification, light intensity, wind speed, and wind direction. When *Cladophora* accumulates at the littoral zone of the lake, they can be salvaged with stationary equipment [55]. However, such physical techniques may not cause damage and destruction to the cells [56], and *Cladophora*, which is not entirely salvaged or intercepted, will continue to grow and reproduce. Physical shading and algae control technology utilize the control of incident light illumination in the water column so that the light level obtained by the *Cladophora* does not satisfy their need to inhibit the growth of *Cladophora* [57] for photosynthesis. The main carriers of photosynthesis are photosystem I (PSI) and photosystem II (PSII) in *Cladophora*, which absorb light energy and transfer energy to PSI and PSII to complete the energy conversion process. Intense light reduces the electron transfer rate in *Cladophora* cells. Also, it causes damage to proteins in the cellular photoreaction center to outpace the rate of light repair, which greatly reduces photosynthetic activity [58]. In recent decades, it has been considered as one of the physical methods to inhibit algal blooms in specific water environments. Using physical shading and ultrasound to destroy algal cells is a common treatment method. It has been shown that physical methods such as shading and ultrasound can cause damage to cell membranes and breakage of organelles, thus disrupting the life activities of algae and affecting their growth and reproduction [59]. In addition, shading and ultrasound can cause chemical reactions within the algal cells, such as inhibition of photosynthesis and inactivation of enzymes, thus further destroying the cell structure. The advantages of the ultrasonic method are simple operation and high efficiency. In addition, this method also makes it difficult to cause secondary pollution. Ultrasonication has been found to disrupt the cellular structure of different planktonic algae, such as the air cells of *Cyanobacteria* [60]. According to the structure of the cells of *Cladophora*, ultrasonication may damage the cell structure of *Cladophora* to a certain extent. Therefore, after considering this, along with the current research and the characteristics of the cells of *Cladophora*, an ultrasound was used as an example to explore the damage mechanism of *Cladophora* cells under physical action (Figure 3).

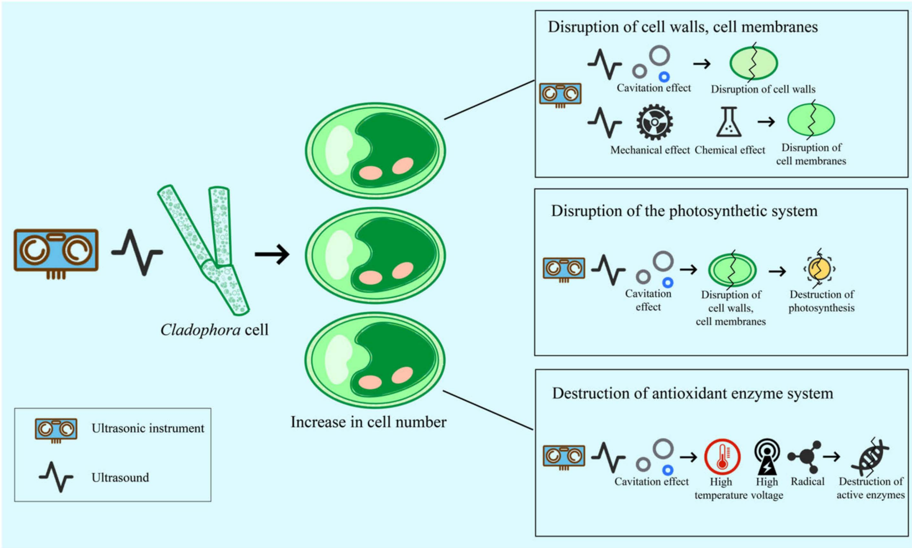

Figure 3. Possible damage destruction mechanism of *Cladophora* cells by physical methods: an example of the ultrasonic technique.

4.1.1. Disruption of Cell Walls and Cell Membranes

Physical methods (such as performing ultrasounds) can cause damage to the cell walls and *Cladophora* cell membranes of *Cladophora*. The effects of ultrasound treatment on algal cells are reflected in changes in their physiological structure and function. Free radicals generated by ultrasound radiation can induce lipid peroxidation to destroy cells [61]. Ultrasonic radiation disperses aggregated algal cells [62], which increases cell number and destroys the cellular structure of *Cladophora*. Based on the study of the effect of ultrasound on the growth and reproduction of algae. The role of ultrasound in controlling water pollution is mainly due to its cavitation effect. The intensity of ultrasound can break the cell wall so that the material inside the cell outflow [63]. Ultrasound is a type of sound wave that produces high-frequency mechanical vibrations, the energy of which can be absorbed by the cell wall and converted into thermal energy [58]. This thermal energy can lead to cell wall rupture and damage, especially in the case of *Cladophora* cells, which have thick cell walls that ultrasound can effectively destroy. By generating a robust mechanical effect, it produces destructive cracks in the cell wall, thus causing the rupture of the cell membrane. Therefore, both mechanical and chemical effects caused by ultrasound may damage the cell wall and cell membrane of *Cladophora*, breaking the cells and releasing intracellular substances [64].

4.1.2. Disruption of the Photosynthetic System

Physical methods can cause damage to the system of photosynthesis in *Cladophora*. Photosynthesis is an essential pathway for *Cladophora* to obtain energy for growth and maintain life activities [65,66]. Ultrasound, for example, inhibits the growth rate of *Cladophora* by disrupting cell walls and cell membranes through cavitation, interrupting photosynthesis, and inhibiting cell division and cell cycle [67]. When an ultrasound is applied to *Cladophora*, the morphology and structure of the chloroplast membrane are significantly altered, and the electron transport chain of photosynthesis is inhibited, causing a failure in the light's reaction. Ultrasounds can produce strong vibrations and a rotation in the light and system of the *Cladophora*, which, thus, destroys the protein structure and electron transport chain required for photosynthesis and decreases the efficiency of photosynthesis and growth rate. Ultrasounds can also cause tiny cavities and cracks in the cells of *Cladophora*, further aggravating the destruction of its photosynthesis. At the same time, ultrasounds can also affect the cyst-like membranes in chloroplasts so that the cell's supply of nutrients is affected. In addition, an ultrasound can also cause the cellular vacuole to collapse, resulting in the over-flow of cytosol, further affecting photosynthesis. Current studies have mainly investigated the effects of ultrasounds on the photosynthesis system in algal cells by measuring the chlorophyll and net photosynthetic oxygen release rate of algal cells [68,69]. In one study, after an ultrasound treatment, the photosynthetic system of *Cladophora* cells was disrupted, making it more difficult for cell activity to be restored and removed [70].

4.1.3. Destruction of Antioxidant Enzyme System

Physical methods also damage the antioxidant enzyme system of the *Cladophora*. Take the ultrasound as an example once again. The high temperature and pressure generated by cavitation and a large number of free radicals can destroy the active enzymes (e.g., superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and glutathione reductase (GR)) and active substances in algal cells, thus affecting the physiological and biochemical activities of the cells [71]. Ultrasounds can disrupt the normal functioning of the antioxidant enzyme system by generating high-energy sound waves, which can have a mechanical impact on the cells, leading to cell membrane rupture and damage to organelles. Ultrasounds can generate large amounts of heat, which can lead to an increase in intracellular temperature that can disrupt the structure and function of the cell. The antioxidant enzyme system is usually temperature sensitive, so ultrasounds may damage its structure and function through thermal effects. Therefore, prolonged ultrasound treatment can also affect *Cladophora* by disrupting their cell membranes, leading to leakage of intracellular enzymes and impairing enzyme activity [72,73].

4.2. Mechanisms of Cell Damage and Destruction of Cladophora under Chemical Action

The chemical method mainly utilizes chemicals to destroy the cell structure of the *Cladophora*, thus leading to its death. This method entails adding chemicals through the water body, such as a variety of algaecides and flocculants, to inactivate the *Cladophora*. At the same time, the redox potential of water that contains algae is changed, and the *Cladophora* colloids are destabilized to achieve the purpose of *Cladophora* removal [74]. The algaecides commonly used include metallic substances (e.g., $CuSO_4$ and copper-containing chelates), oxidizing agents (e.g., $KMnO_4$, O_3, H_2O_2, and ClO_2), and herbicides (e.g., metsulfuron-methyl and bensulfuron methyl) [75]. The primary mechanism of chemical damage to algae cells is to directly or indirectly damage the physiological and genetic structures through different chemicals, causing changes in cell membrane permeability and protein denaturation, which leads to algae cell death or growth inhibition [76]. It has been found that algae cell walls contain large amounts of cellulose and algal-specific gums that maintain the morphology and structure of algal cells [77]. Chemistry can disrupt these structures, making algae cells more fragile. Chemicals can inhibit the photosynthesis of algae cells, reducing the growth rate and metabolic rate of the algae, thus inhibiting the growth and reproduction of the algae. Chemicals can also damage the cell membranes of algae cells, causing substances to leak out of the algae cells, which can lead to the death of the algae cells. In addition, chemicals can destroy the genetic material of algae cells so that the algae cells cannot divide and reproduce normally, thus achieving the purpose of controlling the growth and reproduction of algae [78]. Therefore, according to the structure of *Cladophora* cells, this section mainly focuses on the mechanism of damage and destruction of *Cladophora* cells by chemicals, and the mechanism is shown in Figure 4.

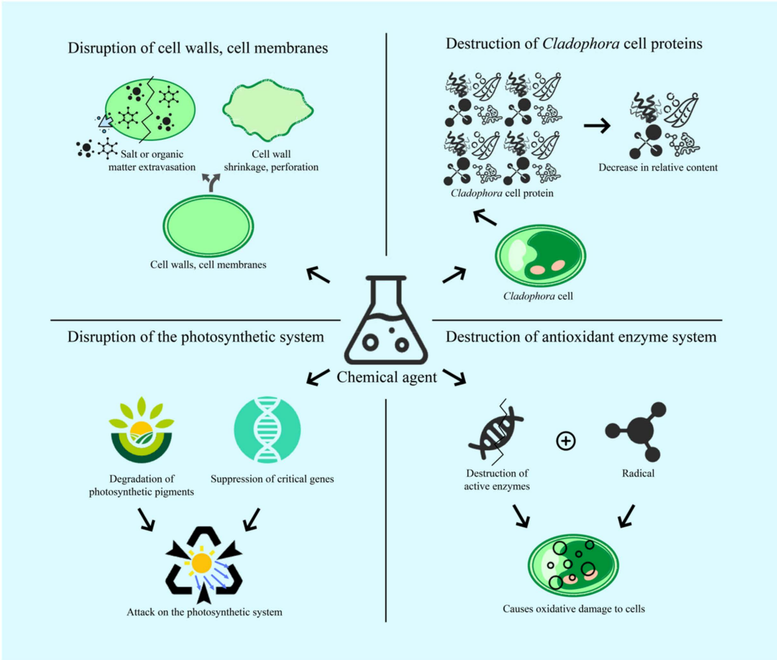

Figure 4. Mechanism of cell damage destruction by chemical agents on *Cladophora*.

4.2.1. Disruption of Cell Walls and Cell Membranes

Chemical damage to *Cladophora* cells is reflected in the cell wall and cell membrane. Chemicals can affect the cell wall, leading to changes in cell membrane permeability, which in turn kills the algal cells [79]. Treatment of *Cladophora* with high dosages of chemicals can cause severe damage to their cell membrane integrity, leading to extravasation of intracellular salts or organic matter. Chemicals can disrupt the structure of the cell wall and the permeability of the cell membrane by destroying the components of the cell wall and the cell membrane. This can lead to the efflux of substances from the cell, such as cellulose and proteins, which can lead to cell death. Chemicals can release organic acids that penetrate the cell walls and membranes of *Cladophora* and react with the cellulose and proteins in them, leading to the rupture and breakdown of the cell walls and membranes. The surface of the cells of *Cladophora* is flat and smooth [80], but after treatment with chemicals, the surface of the cells appears to be wrinkled. The cell wall was shrunk and perforated, and its shape became an irregular ellipsoid. There was also a large amount of flocculent material around the cell wall.

4.2.2. Destruction of Algal Cell Proteins

Chemicals can cause damage to *Cladophora* cell proteins. Algae are rich in protein resources, and the protein content in algae varies depending on the species and season [81]. The cellular protein content of *Cladophora* varied with seasonal changes, and the relative protein content of algal cells showed a significant fluctuating decrease after chemical treatment. Chemicals increase protease activity in *Cladophora* cells, which disrupts the structure of proteins and causes them to lose their original properties and functions. Hydrolyzing the peptide bonds in the protein molecules, the proteins are broken down into smaller peptide segments or amino acids. The administration of chemicals can promote the level of membrane lipid peroxidation in cells, leading to the accumulation of malondialdehyde (MDA) in the cells of *Cladophora* [82]. Accumulation of MDA causes cross-linking polymerization of life macromolecules such as proteins and nucleic acids. It also destroys the structure of the cell membrane, leading to a decrease in the metabolic activity of the cell and affecting the average growth and division of the cell.

4.2.3. Disruption of the Photosynthetic System

Chemicals can likewise cause damage to the photosynthetic system of *Cladophora*. Chemicals attack the photosynthetic system by degrading photosynthetic pigments and inhibiting the expression of critical genes. This results in the inability of the *Cladophora* to properly synthesize photosynthetic pigments such as chlorophyll, thus affecting the process of photosynthesis [83]. By inhibiting the activity of photosynthetic enzymes, the process of photosynthesis is hindered. It can directly damage the structure of the photosynthetic membrane of *Cladophora*, leading to the impaired function of the photosynthetic membrane. In addition, chemicals can interfere with the photosynthetic electron transfer process, resulting in a disruption of the energy production of photosynthesis. Basic metabolic activities such as photosynthesis are impeded, thus blocking the energy capture pathway of the bristlecone algae cells and accelerating cell death. Pigment content is also closely related to photosynthesis, with Chla gradually decreasing as algal cell mortality increases [84]. It is noteworthy that Chla directly affects the capture and utilization of light energy and must be involved in the subsequent conversion of light energy to chemical energy.

4.2.4. Destruction of Antioxidant Enzyme System

The damage that chemicals can do to *Cladophora* is also reflected in damage to the antioxidant enzyme system. Chemicals can damage the antioxidant enzyme system of *Cladophora* cells and produce large amounts of free radicals that cause oxidative damage to the cells [85]. Chemicals can react with enzyme molecules in the antioxidant enzyme system, altering their structure and function, thus affecting the proper functioning of the antioxidant enzyme system. Chemicals may also affect the expression and activity of the antioxidant enzyme system by affecting intracellular signaling pathways. High concentrations of chemicals inhibit enzyme activity, and low concentrations promote enzyme activity [86]. When the concentration of chemicals exceeds a specific range, it will damage the antioxidant mechanism of *Cladophora*. The antioxidant enzymes in the cells cannot clean up the rapidly produced large amount of free radicals in time, which disturbs the metabolism of the cells and even causes the death of Cladophora cells. This led to the phenomenon that the activities of SOD, POD, and CAT first increased and then decreased [87].

4.3. Mechanisms of Cell Damage and Destruction of Cladophora under Biological Action

Biological methods include using aquatic plants, animals, and microorganisms to control algae. Traditional biological means of algae control are mainly aquatic animal control, which utilizes competition or predation among organisms and introduces other organisms to inhibit algal growth [88,89]. The hypophthalmichthys molitrix, which feeds exclusively on plankton and can be used for water purification, has rapidly colonized the Great Lakes and surrounding water systems in North America, causing devastating disasters in the local ecosystems [90]. Microbial algal control includes viral algal control, protozoan algal control, and bacterial algal control [91]. Aquatic plant algal control is a more researched method, which mainly utilizes specific aquatic plants in the water to inhibit algal growth by absorbing, transporting, and metabolizing nutrient-rich substances. Or utilizes the chemosensory inhibition of aquatic plants to control the presence of algae [83]. The main mechanisms of aquatic plant chemosensory substances to inhibit algae include alteration of algal cell enzyme activity, effects on photosynthesis, destruction of algal cell structure, and effects on the ultrastructure of the cell [92]. The *Cladophora* cells also have structures such as cell membranes and photosynthetic systems. The aquatic plant algal control method will have similar inhibitory effects and mechanisms on *Cladophora* cells. Therefore, this section mainly focuses on the damage destruction mechanism of aquatic plant algae control on *Cladophora* cells, and the mechanism is shown in Figure 5.

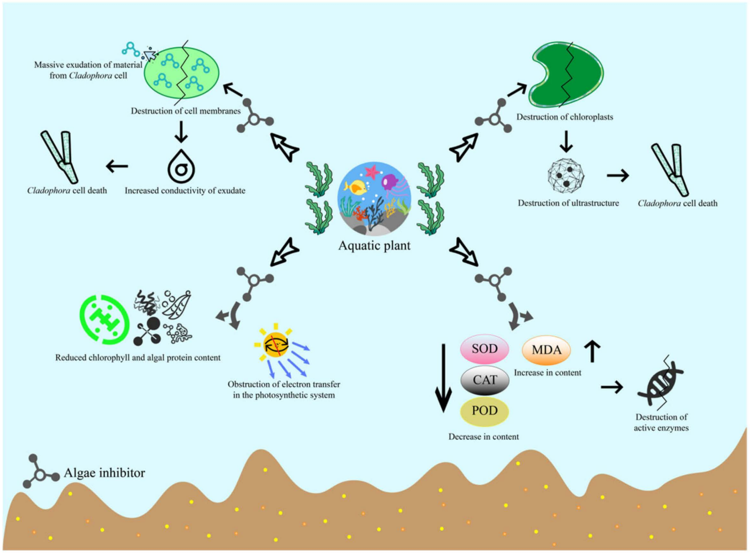

Figure 5. Mechanism of cell damage destruction by aquatic plant algae control on *Cladophora*.

4.3.1. Disruption of Cell Walls and Cell Membranes

Aquatic plants can cause damage to the cell walls and membranes of *Cladophora*. Plants directly or indirectly affect other plants by releasing algae control substances into the environment. Algae-suppressive substances can disrupt cell membranes, reducing their integrity and leading to the exudation of large quantities of intracellular material, increasing the conductivity of the exudate [93]. Studies have shown that lysine contained in algal inhibitory substances can cause a physiological stimulation signal to algal cells, causing algal cells to rupture and cell membrane lysis. Leakage of inclusions also occurs, resulting in apoptosis and achieving the effect of algal inhibition [94]. Due to changes in the permeability of the cell membrane, the cell membrane is prone to take up nutrients from the environment, and exceeding the threshold of the cell membrane will destroy the cell membrane [95]. Para-hydroxybenzoic acid can cause a significant increase in the production of oxygen radicals in algal cells, and free radicals such as O^{2-} can quickly react with cell membrane components, causing damage to the cell membrane and ultimately leading to cell death [96]. Phenolic acids can affect the structure and function of algal cell membranes, causing changes in membrane integrity and permeability [97]. Aquatic plants can secrete several enzymes, including cellulases, amylases, and proteases, which can break down protein, polysaccharides, and lipid molecules in the cell walls and cell membranes of *Cladophora*, thus destroying the structure and function of *Cladophora*.

4.3.2. Destruction of Ultrastructure

Notably, aquatic plants can cause damage to the ultrastructure of *Cladophora* cells. When the cell membrane is damaged, the organelles, such as chloroplasts, are also damaged, and the ultrastructure present in them is damaged. Various physiological activities of the cell are impeded, and the cellular operating system collapses, ultimately leading to cell death and inhibiting the growth of algae [98]. This method has a significant destructive impact on other algae. Studies have shown that the cell shape of *Microcystis aeruginosa* changed irregularly after treatment. The cell membrane began to deform and crumple until rupture, the central nucleoid region was inconspicuous until it disappeared, and the chlorophyll-like vesicles were evident from the previous lamellae [99]. Many ultrastructures, such as nuclei and protein nuclei, existed in the cells of *Cladophora*. Aquatic plants cause the cells to swell and rupture, releasing enzymes to further damage the *Cladophora* cells. Therefore, the method will damage the ultrastructure of the *Cladophora* cells.

4.3.3. Disruption of the Photosynthetic System

Aquatic plants can similarly cause damage to the photosynthetic system of *Cladophora* cells. Photosynthesis is the most critical physiological and biochemical process in algal cells. Inhibition pathways mainly include reducing chlorophyll and phycobiliprotein content and blocking electron transfer in the photosynthetic system [100]. Biological algal inhibition can be achieved simultaneously by blocking the photosynthetic system electron transfer to achieve the effect of algal inhibition. Electron transfer plays an important role in maintaining normal photosynthesis in algal cells. Electron transfer is driven by a redox potential difference between the donor and acceptor sides of PSII. Water is used as a donor of reduced hydrogen to synthesize ATP, which provides energy for the activity of the *Cladophora* cell [101]. Phenolic compounds in plants can reduce protein levels in *Cladophora* cells, thereby reducing their photosynthetic capacity. In addition, respiration in plants can release gases such as carbon dioxide and methane that are detrimental to the growth of *Cladophora*, further disrupting the photosynthetic system.

4.3.4. Destruction of Antioxidant Enzyme System

Aquatic plants also cause some damage to the antioxidant enzyme system of *Cladophora* cells. The antioxidant system consists of an enzymatic scavenging system and a non-enzymatic scavenging system, in which the enzymatic scavenging system is mainly an antioxidant enzyme. These include major antioxidant enzymes such as CAT, POD, GR, aseorbate peroxidase (ApX), and SOD, which enhance plant stress tolerance [102]. The inhibitory effect of most of the substances is manifested by making a decrease in the content of SOD, CAT, and POD and an increase in the content of MDA. Aquatic plants attack the antioxidant enzyme system of *Cladophora* cells by secreting toxins or enzymes. These enzymes can react with the antioxidant enzyme system in the *Cladophora* cells and inactivate it. Aquatic plants can also secrete some organic acids, phytohormones, and other substances. These substances can inhibit the growth and metabolism of *Cladophora* cells, thus further destroying their antioxidant enzyme system.

5. Integrated Control and Potential Utilization Pathways for *Cladophora* Cells

Different control measures can cause different levels of damage to *Cladophora* cells. Based on the damage mechanism of physical, chemical, and biological methods to the cells of *Cladophora*, the study proposes a potentially comprehensive measure for the control of *Cladophora* (Figure 6). This measure gives suitable control measures for different growth periods of *Cladophora*. During the sporulation period, the main structures of *Cladophora* are the cell wall, cell membrane, and nucleus. Ultrasound and chemicals were chosen based on their mechanisms of destroying the cell wall, cell membrane, and nucleus of *Cladophora*. Ultrasound can effectively destroy the cell wall and cell membrane of *Cladophora* spores due to its high mechanical strength. Some chemicals can cause irreversible damage to the nucleus of *Cladophora* spores. However, the environmental friendliness of these chemicals and their potential to cause secondary pollution must be considered. Therefore, for different water environment needs, the two methods can effectively destroy the cell structure of *Cladophora* spores, making it difficult to grow and achieve the effect of prevention and control. After the growth of the *Cladophora*, its cell structure is more complete, and it is necessary to use a variety of methods in combination to destroy the cell structure and inhibit its growth effectively. Based on the mechanism of destroying the photosynthetic system, cell membrane, cell wall, proteins, enzyme system, and ultrastructure of *Cladophora*, various control methods were selected. Shading affects the photosynthetic system by inhibiting photosynthesis in the cells of *Cladophora*, preventing it from obtaining nutrients and fundamentally inhibiting its growth. Ultrasonic waves will disperse the aggregated *Cladophora* cells, thus increasing the number of cells, destroying cell walls and membranes, and improving the removal rate. After UV treatment, it will lead to the blockage of DNA replication and a decrease in the protein content of the *Cladophora* cells, which can not meet the demand for growth of the *Cladophora* cells. Micro-current inhibition will lead to the oxidation of intracellular enzymes, damage to enzyme activity, and the destruction of the enzyme system, thus inactivating the cells. Aquatic plants can damage the ultrastructure existing in the cell organelles, hinder the cell's physiological activities, cause the cell operating system to collapse, and ultimately lead to cell death. Therefore, the use of various methods is effective in destroying the cells of *Cladophora* and causing their apoptosis. In the future, according to the requirements of the water body, further combined with the reproduction and growth of bristle algae factors affecting the regulation. The use of different methods of combining, optimizing, and engineering practice based on the formation of effective integrated control measures for *Cladophora* outbreaks.

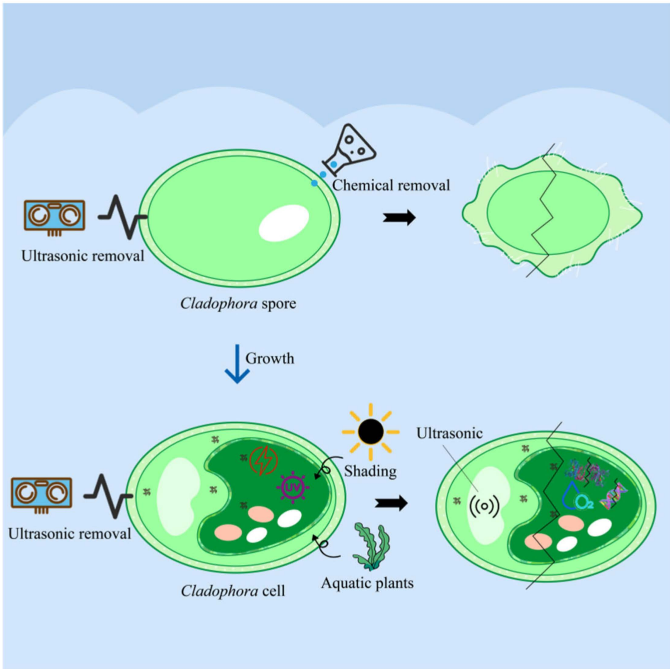

Figure 6. Comprehensive measures for the control of *Cladophora* at different growth periods.

After the cells of the *Cladophora* are destroyed, they are still richly useful. The cells of *Cladophora* are stimulated by the external environment, such as chemicals and temperature changes, which leads to an increase in the permeability of the cell membrane and changes in the activity of proteins and enzymes [103]. The degree of destruction mainly depends on the growth state of the *Cladophora* and environmental factors. For example, the degree of destruction of *Cladophora* is affected by environmental factors such as water quality, temperature, and salinity. *Cladophora* cells are a natural organic fertilizer after being destroyed. It has adsorption capacity, provides nutrients, improves soil texture, promotes plant growth, enhances plant disease resistance, improves plant adaptability, and environmental abatement [104]. It has been found that *Cladophora* is able to accumulate more chemical elements from the environment, which makes them ecologically relevant for wastewater treatment, as well as a potentially high-quality fertilizer product [105]. *Cladophora* cells are rich in proteins, polysaccharides, and fats, which can be extracted as beneficial active pharmaceutical ingredients. In the study of Munir et al., the main activities of algae were described in detail, and Cladophora is a potential raw material for pharmaceutical applications due to its chemical composition [21]. The *Cladophora* cells are also efficient photosynthetic organisms with high oxygen production capacity, which can be converted into biofuel to replace traditional fossil fuels. Dorella et al. proposed the production of biogas by using *Cladophora* mixed with wheat straw [106]. Sharmila and Jeyanthi utilized the biomass of freshwater *Cladophora* for the production of biodiesel [107]. The organic matter and nutrients released from the destruction of *Cladophora* cells also help other organisms to grow and reproduce, thus achieving the effect of ecosystem restoration, as shown by the study of Anh et al. *Cladophora* were used as a protein source when feeding *Penaeus monodon* [108].

6. Conclusions

The *Cladophora* cells are cylindrical, with very thick, rough cell walls. The surface of the spore wall has short and dense setae. The inner layer of the spore wall is a thin membrane which contains the nucleus of the spore. *Cladophora* plays a positive role in maintaining the balance and stability of water ecosystems, but overgrowth can cause damage to water quality. Light is an important environmental factor that influences the distribution of *Cladophora* communities in time and space. Low temperatures in winter and spring inhibit the growth of *Cladophora*. Changes in hydrodynamic conditions can lead to changes in water column material transport, which can affect the growth of *Cladophora*. The biomass of *Cladophora* decreased with increasing water depth. Nutrient salt concentration affects its physiological and biochemical conditions. The *Cladophora* are strong bicarbonate utilizers and are more tolerant to alkaline environments, and pH can control the growth of the *Cladophora*. The process of cell spreading of *Cladophora* is affected by temperature, light, water quality, hydrodynamics, and biological factors.

In order to discuss further the preventive and control measures for the abnormal proliferation of Cladophora and even the reuse of their cells, the mechanisms of damage and destruction of *Cladophora* cells and spores were investigated. Physical actions, chemicals, and aquatic plants all damage *Cladophora* by disrupting cell walls, cell membranes, photosynthetic systems, and antioxidant enzyme systems. The chemicals destroy the cellular proteins of the *Cladophora* cells. Aquatic plants damage the ultrastructure of the *Cladophora*. In the future, combining various methods will be an effective measure to inhibit the growth of *Cladophora*. Although the cells of *Cladophora* are dead after treatment with multiple techniques, they still have many uses and realize the sustainable use of resources. In the future, combined with the water quality requirements of the water body, as well as the actual conditions of the water environment, a combination of a variety of control methods and devices will be applied to inhibit the growth of *Cladophora*. In addition, the cell damage and destruction mechanism of *Cladophora*, as well as further engineering design and validation of the effect of the basis, may provide an essential basis for the sustainable resources of the *Cladophora* cells.

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