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The role of algae and cyanobacteria in the production and release of odorants in water☆

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ABSTRACT

This review covers literatures pertaining to algal and cyanobacterial odor problems that have been published over the last five decades. Proper evaluation of algal and cyanobacterial odors may help establish removal strategies for hazardous metabolites while enhancing the recyclability of water. A bloom of microalgae is a sign of an anthropogenic disturbance in aquatic systems and can lead to diverse changes in ecosystems along with increased production of odorants. In general, because algal and cyanobacterial odors vary in chemistry and intensity according to blooming pattern, it is necessary to learn more about the related factors and processes (*e.g.*, changes due to differences in taxa). This necessitates systematic and transdisciplinary approaches that require the cooperation of chemists, biologists, engineers, and policy makers.

1. Introduction

Water is an integral component of the environment for the persistence of life on this planet. Rapid urbanization, industrialization, excessive agricultural practices, and increasing consumption of domestic water have led to the deterioration of water quality. A significant shortage of water resources is predicted in the near future due to rapid changes in water quality and the growing demand for clean water. As less than 1% of fresh water is available for human use, its proper conservation and management are necessary for sustainable use.

Progressive eutrophication and pollution of surface water have caused a steady increase in odor incidents related to the blooming of aquatic microorganisms in various aquatic environments (Bláha et al., 2009; Hayes and Burch, 1989; Paerl, 1988; Steffensen, 2008; Yoo, 1995). The microorganisms in these blooms produce various terpenoids, carotenoid derivatives, sulfur compounds, and other volatile organic compounds (VOCs) by algae and cyanobacteria most of which can contribute to odor problems (Fink, 2007; Satchwill, 2001; Van Durme et al., 2013). Aquaculture and fisheries are also affected by odor problems such as the presence of various VOCs like geosmin (Wnorowski, 1992). Algae-derived organic matter includes both intracellular and extracellular types with the potential to cause numerous water quality issues, especially the formation of disinfection byproducts and odorous compounds (Li et al., 2012a). These problems are complicated enough to cause profound socio-economic effects (Watson, 2004).

Herein, we provide a review of the multifaceted aspects of odors derived from algal and cyanobacterial species. The production of such unwanted pollutants can pose serious threats to human health and deteriorate the aesthetic quality of drinking water. Other aquatic microorganisms, such as actinomycetes, can also contribute to odor generation in various aquatic environments; however, in this review, the emphasis has been laid mainly on algal and cyanobacterial species. To this end, we attempt to describe the basic factors that exert controls on various types of algal and cyanobacterial odors and their generation. We also discuss the technical approaches required for the proper treatment of algal and cyanobacterial odors in light of potential risks associated with a number of metabolites released in the form of VOCs.

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2. Types of odors from algae and cyanobacteria

Most problems associated with odor are anthropogenic in nature, although some naturally occurring mineral salts (*e.g.*, sulfates and hydrogen sulfide) can also contribute to the production of such components. It was previously reported that more than 35,000 algal species have been demonstrated to cause aquatic odors, although many of them have yet to be characterized in terms of their effects on human health (Watson et al., 2000).

The types of odor vary in chemistry, intensity, and production patterns for different taxa. It has been indicated that odor problems in water supplies can be caused by algae (Dodds et al., 2009; Pretty et al., 2003). Therefore, it is critical to learn more about the type of algal species that are responsible for releasing odors or VOCs.

The major odorous components derived from most algae and cyanobacteria are commonly identified as terpenoids, carotenoid derivatives, fatty acid derivatives, and sulfur compounds (Watson, 2004). Among numerous algal and cyanobacterial odorants, geosmin and 2-methylisoborneol (MIB) with earthy/musty odors have been widely studied (Watson et al., 2008; Zaitlin and Watson, 2006). Geosmin is known to be produced by a variety of cyanobacteria species such as *Oscillatoria*, *Lyngbya, Symploca*, and *Anabaena* (Smith et al., 2008). Geosmin-producing *Anabaena solitaria* caused earthy odors (Wnorowski and Scott, 1990). Geosmin was also produced by *Oscillatoria simplicissima* (recently renamed *Planktothrix pseudagardhii*) and *Anabaena scheremetievi*, causing earthy/musty odors in water (Conradie et al., 2008). It was demonstrated that cyclization of farnesyl diphosphate to geosmin is catalyzed by geosmin synthase via three steps (farnesyl diphosphate to germacradienol, germacradienol to 8,10-dimethyl-1-octalin, and 8,10-dimethyl-1-octalin to geosmin) in cyanobacteria (Giglio et al., 2008). Incidents involving geosmin were noted in Vaal Dam, Klipvoor Dam, Bospoort Dam, and Wentzel Dam in the northern part of the Republic of South Africa. In all of these cases, *Microcystis aeruginosa* was found to be the most prominent microorganism present at the time of odor formation (Wnorowski and Scott, 1990). Three *Oscillatoria* strains and one *Anabaena* species were isolated from three different water supply systems in California that had experienced earthy/musty odor problems in their drinking water (Izaguirre et al., 1982).

MIB was known to be a metabolite of only certain actinomycetes until 1975, when different species (*e.g.*, *Hyella* sp., *Jagerinema genimatum*, and *Oscillatoria variabilis*) that were capable of releasing MIB were identified (Smith et al., 2008). The MIB synthesis in cyanobacteria consist of two important reactions (Giglio et al., 2011). First, geranyl diphosphate 2-C-methyltransferase catalyzed methylation of geranyl diphosphate, C10 monoterpene precursor, into 2-methylgeranyl diphosphate. Second, MIB synthase catalyzed cyclization of the 2-methylgeranyl diphosphate to MIB. Odors of biological origin were first noted in 1969 in the Yodo River basin, which includes Lake Biwa, Japan (Toui, 1991). Initially, these incidents were caused by the MIB-producing strain of *Phormidium tenue*, but the geosmin-producing strain of *Anabaena macrospora* was also isolated in 1981 (Yagi et al., 1983). Later, a strain of *Oscillatoria tenuis*, possessing significant MIB production, was identified (Negoro et al., 1988). Geosmin concentrations decreased along the river course, while the MIB level was not affected, probably due to its resistance to biodegradation (Hishida et al., 1988). Two MIB-producing cyanobacteria (*Oscillatoria germinate* and *Oscillatoria limnetica*) and three geosmin-producing cyanobacteria (*Oscillatoria amoena*, *Oscillatoria splendid*, and *Aphanizomenon flos-aquae*) were identified as sources of undesirable odor in these cases. In addition, benthic *Oscillatoria chalybea* was found to induce earthy smells (Tucker, 2000). *Oscillatoria curviceps* and *Oscillatoria tenuis*, also produce MIB resulting in earthy/musty odors in water (Conradie et al., 2008).

Both geosmin and MIB exhibit strong resistance to oxidation, which is a process routinely applied in water purification. This, combined with their extremely low odor threshold values, makes them the foremost nuisance substances in odor incidents. Numerous cases of these odor incidents have been reported in North America, Japan, Australia, Europe, and China (Su et al., 2015).

The cyanobacteria synthesize geosmin/MIB through their isopernoid pathways via either mavelonic or non-mavelonic pathways during growth. These cyanobacterial cells release or store odorants depending on the growth phase and environmental factors (Watson et al., 2016). Most of the geosmin/MIB is released during the death and biodegradation of these cells. However, there has been immense difficulty in identifying these materials from environmental samples due to difficulties in isolating and maintaining pure strains of cyanobacteria. Some of the geosmin/MIB-producing cyanobacteria can be used to generate axenic cultures. As geosmin/MIB production is not species-specific, genetic markers (*e.g.*, 16S rRNA regions) are not useful in discriminating between potential producers and non-producers. In order to overcome these problems, intensive researches in next-generation sequencing technologies have been performed to elucidate the genes and enzymes involved in the metabolic routes of geosmin and MIB production. This bioinformatic information can be used to quantify the geosmin/MIB production potential in various aquatic environments as well as the chemical synthetic mechanisms responsible for the generation of odorous chemicals (Otten et al., 2016). Polymerase chain reaction (PCR) methods used to target the genes coding for geosmin synthase and MIB synthase involved in geosmin and MIB syntheses, respectively, have been useful for identifying geosmin/MIB-producing cyanobacteria (Kim et al., 2014; Suurnäkki et al., 2015; Wang et al., 2015b).

Algal cells store and/or release geosmin and MIB, producing variable, often prolonged odor dynamics that depend on the algal strain, the environment, and the growth phase (Rashash et al., 1995, 1996). Cell lysis through senescence, death, or treatment can also increase source-water geosmin and/or MIB via the release of preformed cell metabolites (Peterson et al., 1995). The production of VOCs in Lake Ontario was investigated by Watson (2004), who emphasized that there may be a complex interrelationship among physical, hydrological, and climatic factors. Geosmin and MIB serve as important signals, but they are not indicative of cyanobacteria species composition. In addition, they are not necessarily linked to toxin-producing taxa (Watson, 2003a). Therefore, metabolites may not act as a proxy for algal composition.

β-Cyclocitral (a tobacco-smelling substance of the norcarotenoid group) is often found in eutrophic waters, which is the most dominant VOC of all species of *Microcystis* (a genus of cyanobacteria in freshwater) (Jüttner et al., 2010; Ozaki et al., 2008). In addition, β-cyclocitral is involved in the blue-color formation caused by the lysis of cyanobacteria in natural environments. This chemical has been confirmed to originate from *Microcystis* while exhibiting lytic activity against *Microcystis* itself but not for other algae (Arii et al., 2015; Tomita et al., 2016). Also, it is known that *Microcystis aeruginosa* causes a fruity odor resulting from β-ionone (Zhang et al., 2016). Alkyl sulfides and the β-carotene derivative β-cyclocitral often produce these odors in surface waters; certain noxious cyanobacteria species are the major sources of these compounds (Jüttner, 1984b). Also, β-cyclocitral causing musty/tobacco smell was generated during the death of *Microcystis* spp. via enzyme-mediated catalysis (Jüttner, 1984a). It was also reported that β-cyclocitral and β-ionone are released by green algae (*e.g.*, *Ulothrix fimbriata*) (Fink et al., 2006b).

Algal polyunsaturated fatty acid (PUFA) derivatives have been

considered as a potent odor agents in water supplies with the smell of fishy/rancid/cucumber (Watson, 2003b; Watson et al., 2001). n-3 and n-6 PUFA are regarded as important nutritional resources because the desaturation of fatty acid at n-3 and n-6 positions is limited to algae (Cook, 1996; Watson et al., 2009). The cucumber odor produced by *Synura* was found to be caused by 2,6-nonadienal (Wee et al., 1994). Some PUFA derivatives act as either sexual pheromones or in chemical defense against micrograzers in a system that is similar to the response in higher plants induced by wound (Jüttner, 2001; Pohnert, 2000). Chrysophytes isolated from an artificial reservoir (drinking water source) and a mesotrophic pond, such as *Dinobryon cylindricum*, *Uroglena* cf. *americana*, and *Mallomonas papillosa*, have been found to produce diverse odorous compounds such as 2,4-heptandienal (25 μg L^{-1}), 2,4-decadienal (0.3 μg L^{-1}), and 2,4,7-decatrienal (1 μg L^{-1}) (Paterson et al., 2004; Watson and Satchwlll, 2003). Filamentous cyanobacteria (*e.g.*, *Calothrix*, *Plectonema*, *Phormidium* sp. and *Rivularia* sp.) produced a wide range of PUFA derivatives including 1,3,3-trimethyl-2,7-dioxabicylo(2,2,1)heptane (TDH) and 6-methyl-5-hepten-2-one (Höckelmann and Jüttner, 2005). 1-Penten-3-one, 1-penten-3-ol, 2(*Z*)-pentenal, 2(*E*)-pentenal, 2(*E*),4(*Z*)-heptadienal, and 2(*E*),4(*E*)-heptadienal were derived from a green alga, *Ulothrix fimbriata* (Fink et al., 2006b). Moreover, some diatoms (e.g., *Asterionella formosa*, *Achnanthes minutissma*, *Amphora pediculus*, *Cymbella minuta*, and *Gomphonema angustum*) were also seen to excrete 2(*E*),4(*Z*)-heptadienal, 2(*E*),4(*Z*)-octadienal, octa-1,5-dien-3-ol, 1,3(*E*),5(Z)-octatriene, and ectocarpene (Jüttner and Dürst, 1997; Jüttner and Müller, 1979). Other diatoms like *Achnanthes biasolettiana* were seen to release Lipoxygenase products (*i.e.*, oxylipins) (Fink et al., 2006a).

As mentioned above, cyanobacteria are frequent sources of VOCs, while phototrophic non-sulfur bacteria can produce methylated sulfur compounds such as dimethyl sulfide (DMS) and dimethyl disulfide (DMDS) (McCarthy et al., 1993; Steinke et al., 2002). Such organosulfur compounds are fermentation products that are synthesized during cell growth, and they can also cause significant surface water odor because they are insoluble in water (Iliuta and Larachi, 2007). It was found that DMS released from *Emiliania huxleyi* increased by dinoflagellate glazing on the haptophyte alga (Wolfe and Steinke, 1996). Dimethylsuphoninopropionate (DMSP) is formed via enzyme-mediated breakdown upon cell damage, and the cleavage of DMSP results in the production of DMS and acrylate (Wolfe et al., 1997). It should be noted that the release of DMS from ocean and wetland soils has significantly contributed to global sulfur cycling (Gondwe et al., 2003; Watts, 2000). Table 1 summarizes a list of various odorants and species that produce the odorants with their olfactory and organoleptic properties.

Table 2 introduces a list of case studies investigating odor incidents caused by algae and/or cyanobacteria at different locations. Dramatic increases in the nutrient loading in Lake Taihu (the third largest freshwater lake in China) caused by urban and agricultural development in its watershed have accelerated eutrophication; this has led to algal/cyanobacterial blooms (Chen et al., 2003; Duan et al., 2009). In addition, it is well known that cyanobacterial bloom caused mainly by *Microcystis* spp. produced microcystins led to a drinking water crisis in Wuxi, China in late May 2007 (Qin et al., 2010). Researchers collected samples from the Yellow River, which is the source water for six cities, between February and March in 2014 to characterize odorants and algae (Li et al., 2016). A strong fishy odor was detected in Yinchuan city, which was caused by the unusual growth of *Dinobryon*. In the source water of other cities, however, fishy odors were caused by *Synedra*, *Cryptomonas*, *Melosira*, or *Cyclotella*. Saturated aldehydes in the source waters, such as nonanal, benzaldehyde, decanal, heptanal, and hexanal (total concentrations: 690–2166 ng L^{-1}), were responsible for the fishy odors during this season. While DMDS (648 ng L^{-1}) contributed to rancid/swampy odors, geosmin (2.3–9.7 ng L^{-1}) and MIB (5.8–21.1 ng L^{-1}) contributed to earthy/musty odors in the source waters.

3. Methods of detecting algal and cyanobacterial odors

Sensory analysis has been used over long time periods, especially in the assessment of drinking water quality. Threshold odor number (TON) and flavor profile analysis (FPA) are analysis tools recommended by *Standard Methods* (Rice et al., 2012). The TON reflects the maximum level of dilution for a sample at which odor is still perceptible. The FPA method, which uses an undiluted sample, was introduced to overcome the drawbacks of the TON technique and was first designed for food and beverage flavor analysis before being adapted to drinking water. Unfortunately, several limitations to the practical utilization of these techniques have been encountered. For example, sensory evaluation is subjective and difficult to standardize (Meilgaard et al., 2007).

The threshold concentrations of odor from 59 potential drinking water contaminants such as phenol, chlorinated phenolic compounds, aluminum sulfate, pesticides, anisoles, geosmin, and MIB were determined (Young et al., 1996) by adopting the procedures of *Methods for the Examination of Water and Associated Materials* (HMSO, 1982). Their threshold concentrations are presented as geometric mean and as the lowest detected concentration (LDC). The threshold concentrations were also compared with US EPA health standard limits and drinking water guideline values recommended by the World Health Organization. Chemicals with the lowest odor threshold values were found to include (1) geosmin, (2) MIB, (3) chlorinated phenols, and (4) anisoles.

3.1. Instrumental analysis of odorants

Accurate quantification of odorants is essential to evaluate the source and effects of odors in water (Deng et al., 2012). Gas chromatography/mass spectrometry (GC/MS) with extraction techniques and sensory analysis (*e.g.*, flavor-profile analysis) have been used to identify the types and quantities of various odorants.

For the preparation of samples prior to analysis, various extraction techniques using liquid-liquid, Soxhlet, sonication, or pressurized liquid chromatography have been used for the preconcentration of samples. However, most of conventional extraction techniques are expensive, and complicated, while exhibiting low selectivity toward target compounds. A headspace solid-phase microextraction (HSPME) was often recommended as alternative methods for the quantitation of geosmin and MIB in source water and drinking water samples (Watson et al., 2000). A closed-loop stripping analysis (CLSA) technique followed by a large-volume injection for GC/MS was also introduced as an alternative pre-concentration technique to measure earthy/musty odors with analytical sensitivity equal to or better than olfactory sensitivity (Jüttner, 1988; Malleret et al., 2001). Moreover, stir bar sorptive extraction (SBSE) was developed as an alternative option to SPME and CLSA (Baltussen et al., 1999). SBSE provided high sensitivities to geosmin, MIB, and 2,4,6-trichloroanisole (sub-ppt concentration) with good reproducibilities (Nakamura et al., 2001; Ochiai et al., 2001). More recently, needle trap method was developed to more accurately and rapidly analyze various VOCs than conventional extraction techniques (Asl-Hariri et al., 2014; Lord et al., 2010).

The combined application of instrumental and sensory analyses is called chromatographic sniffing (Dattatreya et al., 2002). A capillary column is equipped with an outlet leading to an odor observer. The system is both highly-sensitive and accurate for the determination of retention times. This advance in instrumentation

Table 1
Odorants produced in aquatic algal and cyanobacterial cultures, as reported in previous literatures.

No.	Chemical name	Odor description[a]	OTC (μg L^{-1})[a]	Species to produce the odorant		Reference
				Eukaryotic algae	Cyanobacteria	
1	Dimethyl sulfide (DMS)	Cabbage/sulfurous	1	*Asterionella formosa*; *Nitzschia actinastroides*; *Diatoma elongate*; *Ochromonas danica*; *Ochromonas malhamensis*; *Chlamydomonas globosa*	*Anacystis nidulans*; *Synechococcus cedrorum*; *Oscillatoria chalybea*; *Oscillatoria tenuis*; *Phormidium autumnale*; *Plectonema boryanum*	(Hombeck and Boland, 1998; Ikawa et al., 1992; Ikawa et al., 2001; Jüttner et al., 1986; Watson, 2003b; Watson et al., 2001)
2	Dimethyl disulfide (DMDS)	Septic/garlic/putrid	<4.0	–	*Microcystis aeruginosa*; *Microcystis wesenbergii*	(Hofbauer and Jüttner, 1988; Jüttner, 1984a)
3	Dimethyl trisulfide (DMTS)	Septic/garlic/ putrid/swampy	0.01	–	*Microcystis aeruginosa*; *Microcystis wesenbergii*	
4	Isopropyl disulfide	Alliaceous/onion/ meaty/sulfurous/ cabbage	–	–	*Microcystis flos-aquae*	
5	6-Methyl-5-hepten-2-one	Fruity/ester-like	50.4	*Aulacoseira granulata*; *Cyanidium caldarium*; *Scenedesmus subspicatus*; *Syncrypta* sp.; *Synura* sp.	*Anabaena cylindrica*; *Microcystis aeruginosa*; *Synechococcus* sp.	(Jüttner, 1979; Watson, 2003b)
6	β-Cyclocitral	Tobacco/smoky/ moldy	19.3	*Scenedesmus subspicatus*; *Dinobryon cylindricum*; *Uroglena* sp.; *Ulothrix fimbriata*	*Microcystis aeruginosa*; *Microcystis flos-aquae*; *Microcystis botrys*; *Microcystis viridis*; *Microcystis wesenbergii*	(Fink et al., 2006b; Hofbauer and Jüttner, 1988; Jüttner, 1984a; Watson, 2003b)
7	2-Methylisoborneol (MIB)	Earthy/musty/ camphorous	0.015	–	*Hyella* sp.; *Jaaginema geminatum* (syn. *Oscillatoria geminate*); *Leibleinia aestuarii*; *Oscillatoria curviceps*; *Oscillatoria limosa*; *Oscillatoria tenuis*; *Oscillatoria variabilis*; *Phormidium breve* (syn. *Oscillatoria brevis*); *Phormidium favosum*; *Phormidium tenue* (syn. *Oscillatoria tenuis*); *Phormidium* LM689, *Phormidium* sp.; *Planktothrix agardhii* (syn. *Oscillatoria agardhii*); *Planktothrix cryptovaginata* (syn. *Lyngbya cryptovaginata*); *Planktothrix perornata* f. *attenuate*; *Porphyrosiphon martensianus* (syn. *Lyngbya martensiana*), *Pseudanabaena articulate*; *Pseudanabaena catenata*; *Pseudanabaena limnetica* (syn. *Oscillatoria lill1netica*); *Tychonema granulatum* (syn. *Oscillatoria* f. *granulata*)	(Berglind et al., 1983; Izaguirre et al., 1983; Izaguirre and Taylor, 1995; Izaguirre et al., 1999; Naes et al., 1988; Persson, 1988; Rosen et al., 1992; Sugiura et al., 1997; Tabachek and Yurkowski, 1976; Tellez et al., 2001; Tsuchiya and Matsumoto, 1988; van der Ploeg et al., 1995; Zimba et al., 1999; Zimmerman et al., 1995)
8	Geosmin	Earthy/musty	0.004	–	*Anabaena circinalis*; *Anabaena crassa*, *Anabaena lemmermannii*; *Anabaena macrospora*; *Anabaena planctonica*; *Anabaena solitaria*; *Anabaena viguieri*; *Anabaena millerii*; *Aphanizomenon flos-aquae*; *Aphanizomenon gracile*, *Geitlerinema splendidum* (syn. *Oscillatoria splendida*); *Leibleinia subtilis* (syn. *Lyngbya subtilis*); cf. *Microcoleus* sp.; *Phormidium allorgei* (syn. *Lyngbya allorgei*); *Phormidium amoenum* (syn. *Oscillatoria amoena*); *Phormidium breve* (syn. *Oscillatoria brevis*); *Phormidium cortianum* (syn. *Oscillatoria cortiana*); *Phormidium formosum* (syn. *Oscillatoria formosa*); *Phormidium simplicissimum* (syn. *Oscillatoria simplicissima*); *Phormidium uncinatum*; *Phormidium viscosum*; *Phormidium* sp.; *Planktothrix agardhii* (syn. *Oscillatoria agardhii*); *Planktothrix prolifica* (syn. *Oscillatoria prolifica*); *Pseudanabaena catenata*; *Schizothrix muelleri*; *Symploca muscorum*; *Tychonema bornetii* (syn. *Oscillatoria bornetii*);	(Berglind et al., 1983; Bowmer et al., 1992; Izaguirre and Taylor, 1995; Jüttner et al., 1986; Naes et al., 1988; Persson, 1988; Rosen et al., 1992; Schrader and Blevins, 1993; Sugiura et al., 1997; Tabachek and Yurkowski, 1976; Tsuchiya and Matsumoto, 1988; Watson, 2003b; Wu et al., 1991)

(*continued on next page*)

Table 1 (*continued*)

No.	Chemical name	Odor description[a]	OTC (μg L^{-1})[a]	Species to produce the odorant		Reference
				Eukaryotic algae	Cyanobacteria	
					Tychonema granulatum (syn. *Oscillatoria* f. *granulata*)	
9	β-Ionone	Violets/fruity	0.007	*Cyanidium caldarium*; *Scenedesmus subspicatus*; *Synura* sp.	*Anabaena cylindrica*; *Aphanizomenon gracile*; *Synechococcus* 6911	(Jüttner, 1979; Watson, 2003b)
10	1,2-Dihydro-1,1,6-trimethylnaphthalene	Licorice	–	*Cyanidium caldarium*	–	(Jüttner, 1979; Watson, 2003b)
11	Geraniol	Sweet/floral/fruity/rose/waxy/citrus	77.1	–	*Synechococcus* 6911	(Ikawa et al., 1992; Ikawa et al., 2001; Watson, 2003b)
12	Geranylacetone	Fresh/green/fruity/waxy/rose/woody/magnolia/tropical	0	*Cyanidium caldarium*; *Scenedesmus subspicatus*	–	(Jüttner, 1979; Watson, 2003b)
13	Nerol	Sweet/natural/neroli/citrus/magnolia	293.1	–	*Synechococcus* 6911	(Ikawa et al., 1992; Ikawa et al., 2001; Watson, 2003b)
14	2,4-Decadienal	Rancid/fishy	19.8	*Dinobryon divergens*; *Dinobryon cylindricum*; *Mallomonas papillosa*; *Synura petersenii*; cf. *Syncrypta* sp.; *Uroglena americana*; *Uroglena* sp.; *Fragilaria* sp.; *Cryptomonas rostratiformis*; *Peridinium willei*	–	(Miralto et al., 1999; Watson, 2003b)
15	2,4,7-Decatrienal	Rancid/fishy	19.5	*Dinobryon divergens*; *Dinobryon cylindricum*; *Synura petersenii*; *Uroglena americana*; *Uroglena* sp. (UTCC276)	*Microcystis papillosa*; *Microcystis varians*	(Miralto et al., 1999; Watson, 2003b)
16	Ectocarpene	Tomato-leaf like	–	*Amphora veneta*; *Gomphonema parvulum*; *Phaeodactylum tricornutum*; *Skeletonema costatum*; *Lithodesmium undulatum*; *Ectocarpus spp.*	–	(Boland et al., 1983; Derenbach and Pesando, 1986; Jüttner and Dürst, 1997; Moore, 1976; Watson, 2003b; Wendel and Jüttner, 1996)
17	Dictyopterene A	–	–	*Amphora veneta*; *Gomphonema parvulum*	–	(Boland et al., 1983; Derenbach and Pesando, 1986; Jüttner and Dürst, 1997; Moore, 1976; Watson, 2003b; Wendel and Jüttner, 1996)
18	(*E*,*Z*)-1,3,5-octatriene	Green/plastic	–	*Synura* sp.; *Fucus* sp.; *Asterionella formosa*	–	(Hombeck and Boland, 1998; Jüttner et al., 1986; Watson, 2003b; Watson et al., 2001)
19	4-Methylthio-1,2-dithiolane	–	–	*Chara globularis*; *Chara hispida*; *Chara baltica*; *Nitella translucens*; *Tolypella nidifica*	–	(Watson, 2003b; Wium-Andersen et al., 1982)
20	5-Methylthio,-1,2,3,-trithiane	–	–	*Chara globularis*; *Chara hispida*; *Chara baltica*; *Nitella translucens*; *Tolypella nidifica*	–	(Watson, 2003b; Wium-Andersen et al., 1982)
21	Ketone and ionone derivatives	–	–	–	*Calothrix parietina*; *Rivularia* sp.; *Tolypothrix distorta*	(Höckelmann and Jüttner, 2005; Smith et al., 2008)

[a] (Watson, 1999, 2004; Young et al., 1996).

Table 2
Case studies of odor in aquatic ecosystems.

No.	Place	Species	Odorant concentration (ng L^{-1})	Reference
1	Yodo River originating from Lake Biwa (Japan)	*Anabaena macrospora*	Geosmin MIB	(Hishida et al., 1988)
2	Lake Zürich (Switzerland)	*Aphanizomenon*, *Oscillatoria*, *Planktothrix*	Geosmin (21)	(Durrer et al., 1999)
3	Lake Kamafusa (Japan)	*Phormidium tenue*	MIB	(Oikawa and Ishibashi, 2004)
4	Han River (South Korea)	Cyanobacteria	Geosmin (30) MIB (38)	(Oh et al., 2005)
5	Gonghu Bay of Lake Taihu (China)	*Microcystis aeruginosa*	DMTS (69.6)	(Chen et al., 2010)
6	Nakdong River (South Korea)	*Aphanizomenon*; *Microcystis*	Geosmin (24)	(Lee et al., 2013)
7	Zhushan Bay of Lake Taihu (China)	*Microcystis*	MIB (59.3) β-Ionone (676.8) DMTS (4489.5)	(Wang et al., 2014)
8	Huajiang Reservoir in winter (China)	*Chlorophyta; Cryptophyta; Bacillariophyta*	Geosmin (20–65) MIB (29–102)	(Wang et al., 2015a)
9	Source waters of the Yellow River (China)	*Dinobryon*; *Melosira*; *Cyclotella*; *Cryptomonas*; *Synedra*	Geosmin (2.26–9.73) MIB (5.77–21.12) DMDS (648.2) Saturated aldehydes (690–2166)	(Li et al., 2016)

has been achieved by the combined use of sensory-GC and sensory panel analytical techniques (Suffet et al., 2004).

An SPME-GC/MS and sensory method was applied to quantify odorous compounds in the natural waters of three Swiss lakes; these were identified to be in the sub-ppt to low-ppt range (Peter et al., 2009). Deng et al. reported that this instrument facilitates the extraction of odors from a variety of different matrices (Deng et al., 2012). A rapid and flexible microwave-assisted purge-and-trap extraction device was also used to simultaneously determine five dominant odorants from primary sources and sinks: dimethyl trisulfide (DMTS), 2-methylisoborneol, geosmin, β-cyclocitral, and β-ionone (Deng et al., 2012). The system of SBSE followed by thermal desorption-capillary GC/MS/olfactometry had a good ability of identification and speciation of odorants (geosmin, MIB, 2,3,4-trichloroanisole, 2,3,6-trichloroanisole, 2,4,6-trichloroanisole, and 2,4,6-tribromoanisole) in water samples (Benanou et al., 2003). Seasonal and spatial patterns of odor compounds were investigated at 15 sites in the Gonghu Bay of Lake Taihu in 2008 using a purge-and-trap system coupled with GC/MS (Chen et al., 2010). GC/MS revealed that the maximum amount of particulate DMTS (69.6 ng L^{-1}) exceeded its odor threshold concentration (OTC) (10 ng L^{-1}), and the maximum concentration of dissolved DMTS was 6.1 ng L^{-1}.

It was also demonstrated that Fourier transform infrared (FTIR) microspectroscopy can be used for the in situ, nondestructive, chemical analysis of individual algal cells (Murdock and Wetzel, 2009). Blooms involving *Anabaena*, *Oscillatoria,* and *Aphanizomenon* are present in several bodies of water in Canada and Philadelphia, and the chemical analysis of lake water from these locations revealed the presence of geosmin and β-cyclocitral (Wnorowski, 1992).

3.2. Molecular-based (biological) assays

The discovery of the genes involved in the geosmin and MIB biosynthetic pathways has provided a basis for the development of detection strategies (Jüttner and Watson, 2007). The simplest option is to use PCR for the direct detection of odor producers in various environmental samples. Giglio et al. developed an assay based on the specific gene coding for geosmin synthase (Giglio et al., 2008). This assay is based on the strictly conserved Mg^{2+}-binding motifs of geosmin synthase, DDHFLE and NDLFSYQRE, which are found in the N-terminal domain of all geosmin synthases involved in cyanobacterial geosmin production. The partial degenerated primer 250F (5′-TTCTTCGACGAYCACTTCC-3′) and reverse primer 971R (5′-CCCTYGTTCATGTARCGGC-3′) produced 73-bp DNA fragments from all geosmin producers, including *Geitlerinema* sp., *Nostoc* sp. UTAH12-18b, *Anabaena laxa*, and *Phormidium calcicola*. The same group also confirmed the presence of positive PCR isolates by GC/MS. The authors concluded that the production of geosmin in cyanobacteria results from the presence of a single gene that encodes the geosmin synthase enzyme. Based on this information, a diagnostic geosmin synthase PCR protocol can be developed. This protocol promises to be a valuable tool that will allow water utilities to detect the organisms responsible for geosmin production in any given body of water. The PCR protocol can also differentiate the genus and species of geosmin odor-producing cyanobacteria using the different characteristic melting profiles. Recently, Su et al. established quantitative polymerase chain reaction (qPCR) methods to detect the levels of *Anabaena* sp. and geosmin (Su et al., 2013). These qPCR assays are related to the microscopic cell count results. This assay has the potential to reduce the time for obtaining the results while not requiring the expertise in algal identification and taxonomic.

Similarly, a potential assay for MIB synthase has been developed for MIB producers. Wang et al. reported linear relationships between the number of cells and MIB concentration using a qPCR assay based on the MIB synthase gene (Wang et al., 2016). The study indicated that the assay is very sensitive in the range of approximately 10–60 fg per *mic* copy (DNA-based). The authors emphasized that the linear correlation has the potential to provide a strategy for risk management and early detection in the field. In addition, multiplex assays that can detect several geosmin-producing species and/or MIB-producing species in a single assay will be feasible for industrial use.

Recently, a bioelectronic nose for the real-time assessment of geosmin and MIB was also reported. This tool uses the human olfactory receptor protein (hOR) and a single-walled carbon nanotube field-effect transistor (swCNT-FET) (Son et al., 2015). The bioelectronic nose was able to selectively detect geosmin and MIB at low concentrations (*e.g.*, 10 ng L^{-1}). Furthermore, the detection of these compounds in real water samples including river water, bottled water, and tap water was demonstrated without using any pre-treatment processes.

4. Factors affecting algal and cyanobacterial odors

Various factors may also be inextricably linked to algal and cyanobacterial odors. Temperature, partial pressure of water, and solubility of VOCs are important factors in the production and release of algal odor. The combined effects of these factors can simultaneously affect the production of algal and cyanobacterial odors in water. For

instance, the partial pressure of water in the atmosphere increases with increasing temperature; thus, algal odors can be more prominent in the summer. Note that cyanobacteria are widely tolerant and have varying optimum growth conditions. However, cold temperatures generally inhibit their metabolism (Davis et al., 2009). The geosmin production of *Lyngbya kuetzingii* was observed to be maximized at 10 °C (Zhang et al., 2009).

An excessive amount of algae leads to low dissolved oxygen concentrations in water, which cause algal blooms potentially producing toxins (Bricker et al., 2008). However, some algae are now known to grow well and fix nitrogen under low dissolved oxygen concentrations with high quantities of H_2S (Boyd and Tucker, 1998). The influence of dissolved oxygen concentration on bloom formation is not direct in nature, but may have an indirect effect because oxygen influences the nutrient flux by regulating the redox potential (Silvey et al., 1972). Also, it was reported that atmospheric oxygen is required for unsaturated aldehydes (*e.g.*, 2,4,7-decatrienal) to be formed via lipoxygenase reactions in *Melosira* (Wendel and Jüttner, 1996).

Light is another variable that can affect the production of various VOCs and the growth of divergent algal species. The optimum light intensity for the growth of cyanobacteria (approximately 3.15 W m^{-2}) is usually less than that required for most green algae. However, blue-green algae have been shown to flourish at unmeasurable light intensities; some algae can grow in absolute darkness as long as there is a carbohydrate source (*i.e.*, mixotrophs) (Silvey et al., 1972). Moreover, intense light has been shown to inhibit gas vacuole formation in certain cyanobacteria (Blevins et al., 1995). Several studies have indicated that light is a primary driver for the production of geosmin and MIB (Li et al., 2012b; Saadoun et al., 2001; Zhang et al., 2009). This was recently confirmed by qPCR, which showed a change in the expression of geosmin synthase in a model cyanobacteria (*Anabaena* sp. PCC7120) under a light intensity of about 19 W m^{-2}. Furthermore, the intracellular geosmin level was proportional to the growth of this cyanobacterium.

A previous study reported geosmin production from a common bloom that formed by *Anabaena* (Paerl and Tucker, 1995). The cyanobacterial bloom was favorable when nitrogen availability was limited relative to phosphorus (*i.e.*, high nutrient loading). Milovanović et al. (2015). reported that the concentrations of MIB were higher in all *Anabaena* and *Nostoc* strains that were grown without added nitrogen (−N) compared to the same strains where nitrogen was added to the growth medium (+N). This may indicate that the presence of added nitrogen suppresses the biosynthesis of MIB. It was also shown that the high yield of *Anabaena* sp.-derived geosmin (2.8 μg L^{-1}) was achieved at 123.5 μg L^{-1} of nitrate-N (Saadoun et al., 2001). The geosmin production was correlated with ammonium-N. High ratio of N to P was seen to suppress the production of geosmin.

5. Treatment of odors

Treatment of odor in aquatic ecosystems is required before they can be used as potable water sources, which prevents various health hazards caused by the presence of VOCs (DeZuane, 1997). Therefore, treatment of odors at water supply sources is highly desirable. However, the reliance on a typical sequence of water treatment routes (*i.e.*, coagulation-sedimentation-filtration-chlorination) is not efficient to remove odor from water (Montiel, 1983).

Among various oxidizing agents utilized in the water industry, chlorine (Cl_2) is the most popular oxidant and disinfectant (Wnorowski, 1992). Cl_2 not only provides a long-lasting residual concentration in the distribution system but also is efficient in destroying organic sulfides (Krasner et al., 1989). However, Cl_2 produces odorous byproducts such as medicinal-smelling chlorophenols; in addition, it gives an unpleasant odor to the water when improperly dosed (Wnorowski, 1992). It is known that Cl_2 treatment is not appropriate for geosmin and MIB because oxidation of such odorants hardly occurs by chlorination (Lalezary et al., 1986). Chlorine dioxide (ClO_2), while found to be not efficient for removing hydrocarbons, was useful for removing chlorophenols without the formation of trihalomethane (Walker et al., 1986).

Ozone (O_3) is an option for treating geosmin and MIB compounds despite the generation of a strong fruity odor (Anselme et al., 1988; Ho et al., 2002; Meunier et al., 2006). The use of O_3 with a dosage of 3.8 mg L^{-1} was also reported to efficiently remove musty/earthy odor caused by blue-green algae in a short contact time (~6 min) (Jung et al., 2004). A process of ozonation and biofiltration was tested at a full-scale plant (Nerenberg et al., 2000). In the tandem process, ozonation was capable of partially removing geosmin and MIB, followed by biofiltration of residual geosmin and MIB. The process was also biologically stabile.

Advanced oxidation processes (AOPs) involving both an oxidizer and an agent (*e.g.*, O_3 and UV) have been introduced (Glaze et al., 1990). The processes facilitated oxidation by the formation of free hydroxyl radicals from hydrogen peroxide (H_2O_2) (Andreozzi et al., 1999). These hydroxyl radicals are a more effective oxidant than Cl_2 or O_3, especially toward aliphatic compounds such as geosmin and MIB (Jo et al., 2011; Zoschke et al., 2012). For the AOP systems, peroxone (a combination of O_3 and H_2O_2; O_3-H_2O_2), O_3-UV, and H_2O_2-UV have been employed (Glaze et al., 1990; Kruithof et al., 2007; Rosenfeldt et al., 2005). A pilot scale of O_3-H_2O_2 treatment system was also optimized (Ferguson et al., 1990). Furthermore, various AOPs, such as H_2O_2-UV, O_3, and O_3-UV, have been studied to remove chlorophenols (Pera-Titus et al., 2004). Benzothiazole, mercaptans, sulfides, and aromatic odorants have also been treated by UV-based AOPs at different scales (Antonopoulou et al., 2014).

Activated carbons have been widely used for removing odorants. For small treatment facilities, powdered activated carbon (PAC) is superior to granular activated carbon (GAC) due to its unique characteristics: (1) rapid adsorption equilibrium, (2) no major capital cost, (3) possibility of intermittent application, and (4) low cost per unit mass (Roux, 1989). Alternatively, GAC can be regenerated and used for prolonged time periods before reaching a saturation point, but it requires high installation costs (Çeçen and Aktas, 2011). MIB was shown to be adsorbed on activated carbons less readily than geosmin (Zoschke et al., 2011). Applications of GAC filters in pilot and full-scale plants have been successful (Hattori, 1988; Terashima, 1988; Vik et al., 1988). PAC is normally used in conjunction with sedimentation-filtration procedures (Joubert et al., 1989). The combination of PAC with a dissolved air flotation (DAF) is an alternative technique, which is referred to as the PAC/DAF process (Roux, 1989).

Biological degradation of organic odorants is one of the attractive alternative treatment methods to physico-chemical treatment methods. It was found that *Bacillus cereus* and *Bacillus subtilis* could degrade geosmin (Narayan and Nunez, 1974). However, although efforts were made to isolate the enzyme responsible for the degradation of geosmin, it was not successful (Danglot et al., 1983). In addition, sand filters that are biologically active were used to efficiently remove odors in drinking water (Lundgren et al., 1988). Upon the isolation of *Cabdida* sp. from a slow sand filter, the isolated yeast showed the ability to decompose MIB both in cell form and as a crude enzyme (Sumitomo et al., 1988). It was also shown that biological sand filtration is effective for completely removing geosmin and MIB via biodegradation in a batch-type bioreactor (Ho et al., 2007). In this biodegradation process, the decomposition of geosmin and MIB proceeded in a pseudo first order reaction with a

Table 3
Water treatment processes used to control odors.

No.	Odorant	Efficient treatment	Inefficient treatment	Reference
1	Geosmin	O_3, UV/H_2O_2, O_3/H_2O_2, activated carbon, biological	Cl_2, ClO_2, $KMnO_4$, chloramines, aeration	(Anselme et al., 1988; Ferguson et al., 1990; Glaze et al., 1990; Jung et al., 2004; Kruithof et al., 2007; Lalezary et al., 1986; Rosenfeldt et al., 2005; Wnorowski, 1992)
2	MIB	O_3, UV/H_2O_2, O_3/H_2O_2, activated carbon, biological	Cl_2, ClO_2, $KMnO_4$, chloramines, aeration	
3	IPMP, IBMP	Cl_2, ClO_2, activated carbon	$KMnO_4$, aeration	
4	TCA	O_3, ClO_2, activated carbon, biological	Cl_2, $KMnO_4$, aeration	
5	DMTS, DMDS	Oxidation, activated carbon, biological	Chloramines	
6	Chlorinated compounds	Activated carbon	Biological	
7	H_2S	Aeration, oxidation	–	
8	Low molecular weight aromatic and aliphatic compounds	Aeration, activated carbon	Oxidation	
9	Phenol, chlorophenols	O_3, ClO_2, activated carbon, biological	Cl_2, chloramines, $KMnO_4$	
10	Benthic cyanobacterial bloom	Optimization of water levels in reservoirs	–	(Su et al., 2017)

range of reaction rate between 0.1 and 0.58 day^{-1}. Gel-immobilized enzymes were effective for the removal of MIB, but they required prolonged contact times (20–40 h). It was also reported that mixed bacterial populations consisting mainly of *Pseudomonas* spp. decreased the content of MIB content in water in 7–17 days (Izaguirre et al., 1988a, 1988b). *Thiobacillus thioparus* immobilized on porous propylene pellets was tested for removing the odorants containing sulfur (Tanji et al., 1989).

It was demonstrated that, although black blooms can be suppressed by sediment dredging at an appropriate depth, sediment dredging was unable to suppress the offensive odor of algal blooms (Liu et al., 2015). Guo et al. demonstrated that, although musty odors can be removed effectively in typical water treatment plants by combining ozonation and biological activated carbon, septic odors and associated odorants required further treatment with sand filtration and chlorination for complete removal (Guo et al., 2016). MIB-induced odor caused by *Planktothrix* sp. was reduced by increasing the water level in the Miyun Reservoir, China (Su et al., 2017). When the water level was increased from 131.0 to 147.7 m, an acceptable risk level of 10% was reached. This approach represents a cheaper and simpler water odor management method that does not harm the water environment.

A large variety of odorous substances and the factors controlling their distribution in water indicate the importance of identifying off-flavors before deciding the treatment techniques. Proper and cost-effective treatment method should be determined on a case by case basis. Table 3 lists some of the treatment methods that can be used to address odor-related problems. A diagrammatic representation of odorant treatment options is shown in Fig. 1.

6. Conclusions

Odorants are sensitive indicators to diagnose malfunction in water source and distribution systems. Their presence above certain levels also reflect changes in ecological system resulting from human-related disturbance. Algae and cyanobacteria are the major causes of odors in water. In these regards, this review summarizes various odorants produced in water by algal and cyanobacterial species. In addition, various analytical techniques developed for tracing the odorants and their treatments are summarized. As researches about this area are still limited, we hope that this review should draw many researchers' attention to investigate the practical issues for solving odor-related problems in water.

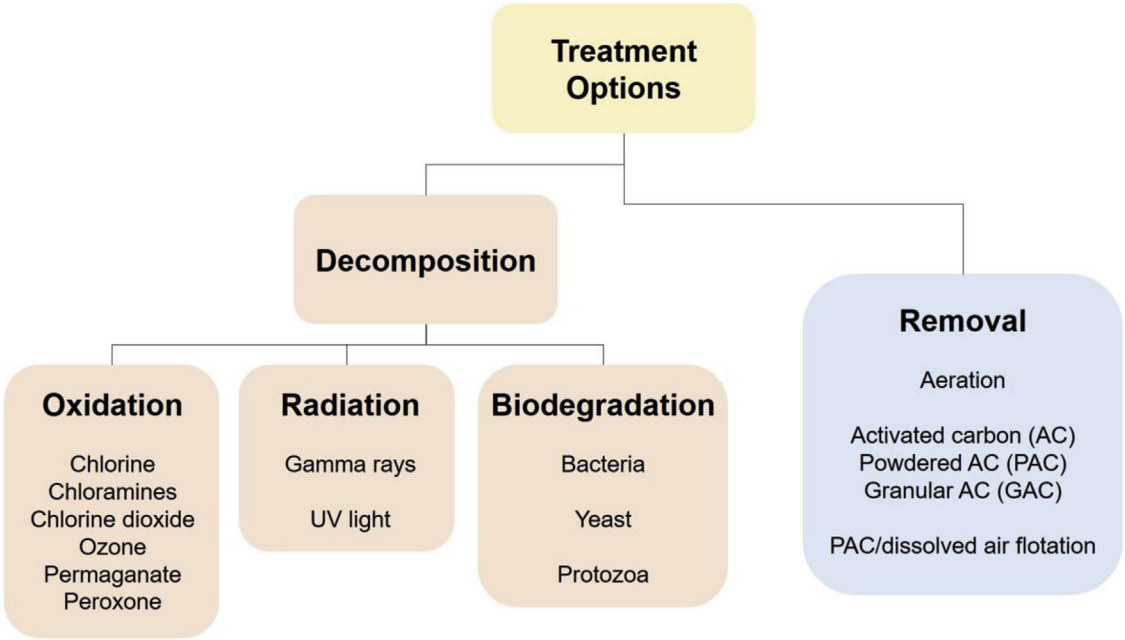

Fig. 1. Algal odor treatment options.

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