Microbially Derived Off-Flavor from Geosmin and 2-Methylisoborneol: Sources and Remediation

Kishore Kumar Krishnani[1], Pitchaiyappan Ravichandran[1], and Subbanna Ayyappan[2]

I Introduction

The occurrence of tastes and odors is a recurrent problem in the beverage, potable water, food, and aquaculture industries. Taste-and-odor (T/O) occurrences have been documented in a number of public water supply reservoirs (Silvey et al. 1950; Suffet et al. 1996) in the United States (Rosen et al. 1970; Izaguirre et al. 1982; Seligman et al. 1992; Burlingame et al. 1986, 1992; Young et al. 1999), Canada (Slater and Blok 1983a, b), Japan (Yagi et al. 1981, 1983; Yagi 1988; Hosaka et al. 1995), Australia (Hayes and Burch 1989; Baker 1992; Baker et al. 1994, 2001), The Netherlands (Piet et al. 1972), Sweden (Lundgren et al. 1988), Germany (Mohren and Jüttner 1983), Finland (Veijanen et al. 1988, 1992), France (Cotsaris et al. 1995), India (Desikachary 1959; Arora and Gupta 1983; Krishnani et al. 2005, 2006a),

[1] Central Institute of Brackishwater Aquaculture, 75, Santhome high road, R.A. Puram, Chennai-600028, India

[2] Krishi Anusandhan Bhavan, Indian Council of Agricultural Research, Pusa, New Delhi, 110012, India

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Taiwan (Lin et al. 2002), and Spain (Sabater et al. 2003; Vilalta et al. 2003, 2004). Food industries, including grapes (La Guerche et al. 2005), apples (Frank 1977; Siegmund and Pollinger-Zierler 2006), pears (Nunes 2002), peaches (Mercier and Jimenez 2004), and vegetables such as dried beans or beetroot (Maga 1987) have also been affected with inconsistent flavor. Based on suspected origins, Tucker and van der Ploeg (1999) and van der Ploeg (1991) categorized off-flavors as rotten, decayed, cardboard, stale, petroleum, fishy, woody, earthy or muddy, and musty. This chapter presents an extensive review of chemical causes of off-flavor problems, especially with reference to muddy and musty flavor in aquatic organisms and possible remediation techniques.

II Chemical Causes of Off-Flavor

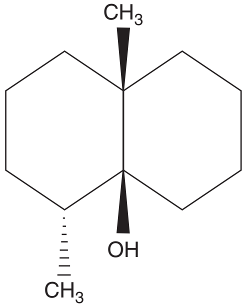
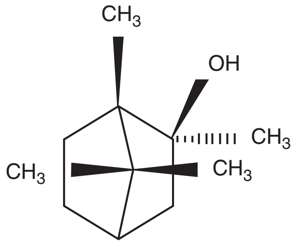
Problems of off-flavors caused by chemicals have been reported for fish (Whitfield et al. 1994) and Crustacea (Whitfield et al. 1981, 1988). Petroleum off-flavors occur mainly from accidental spills of diesel fuel when fish are exposed to persistent petroleum products, causing long-lasting flavor problems (Tucker and van der Ploeg 1999; Motohiro 1983). Rotten and sulfury off-flavors have been attributed to polysulfides formed by decomposition of blooms in freshwater reservoirs in Australia (Hayes and Burch 1989). Dimethyl trisulfide has been correlated with off-flavor problems in cheese, prawns, and vegetables (Hayes and Burch 1989; Whitfield et al. 1981).

Algal volatile organic compounds (AVOCs), mainly terpenoids, cause economic losses to water, food, and aquaculture industries because of reported taste and odor (Wnorowski and Scott 1992; Engle et al. 1995; McGuire 1995; Watson 1999, 2003), which establish chemical communication among organisms (Harborne and Tmoas-Barberan 1989; Harrawijn et al. 2001). The role of natural biofilm inside pipelines as a potential source and reservoir for odorous volatile organic compounds has been well documented (Skjevrak et al. 2005). Watson and Ridal (2003) found that periphyton is a major T/O source in the St. Lawrence River.

A large group of compounds such as 2-methoxy-3-isopropylpyrazine, di-, tri-, tetra-, and pentachloro anisoles, octa-1,3-diene, 2-methylisoborneol, (MIB), and geosmin are responsible for an earthy-musty off-flavor (Kilkast 1993). Schnurer et al. (1999) characterized fungal volatiles from mainly *Aspergillus*, *Fusarium*, and *Penicillium* with gas chromatography, mass spectrometry, and sensory analysis; common volatiles found were 2-methyl-1-propanol, 3-methyl-1-butanol, 1-octen-3-ol, 3-octanone, 3-methylfuran, ethyl acetate, and the malodorous 2-methylisoborneol and geosmin. Fravel et al. (2002) characterized volatile compounds emitted by sclerotia of *Sclerotinia minor* and *Sclerotinia sclerotiorum* and identified as 2-methylenebornane and 2-methylisoborneol by solid-phase microextraction followed by gas chromatography and mass spectrometry.

Because this review focuses mainly on geosmin (*trans*-1,10-dimethyl-*trans*-9-decalol) and 2-MIB (1,2,7,7 tetramethyl-*exo*-bicyclo heptan-2-ol), their chemical

Table 1 Physical and chemical characteristics of geosmin and 2-methylisoborneol (MIB)

Characteristics	Geosmin	2-Methyl isoborneol
Structure		
Chemical name	*trans*-1,10-Dimethyl-*trans*-9-decalol	1,2,7,7-Tetramethyl-exo-bicyclo-heptan-2-ol
Molecular formula	$C_{12}H_{22}O$	$C_{11}H_{20}O$
Formula weight	182.31	168.28
Appearance	Light yellow oil	White solid
Boiling point	270°C	—
Organoleptic properties	Earthy-muddy	Musty
Odor threshold concentration (ng/L)	10	29
Human olfactory sense (ng/L)	4	7–15
Toxicity to rainbow trout (mg/L)	0.45	10
LC_{50} (sea urchin embryos) (mg/L)	17	69

Sources: Cees et al. 1974; Gagne et al. 1999; Gerber 1968, 1969; Nakajima et al. 1996; Persson 1979; Watson et al. 2000.

structures and chemical and physical characteristics are shown in Table 1. Geosmin and MIB implicated in muddy-musty flavors of water and fish are a problem in the aquaculture, food, beverage, and potable water industries. These compounds are reported as a source of musty-earthy flavor in grain caused by improper storage (Wasowicz et al. 1988; Jelen et al. 2003). Geosmin is also known to contribute to a characteristic earthy red beet flavor (Lu et al. 2003) and an earthy smell in grapes (La Guerche et al. 2005). MIB was related to musty-earthy notes in Brie and Camembert cheese flavor (Karahadian et al. 1985). Siegmund and Pollinger-Zierler (2006) detected higher concentrations of 2-isopropyl-3-methoxypyrazine, 2-isobutyl-3-methoxypyrazine, 2-methylisoborneol, 1-octen-3-ol, fenchyl alcohol, geosmin, and guaiacol as well as 2,6-dibromophenol in apple juice samples.

Geosmin and MIB have been reported to be responsible for most source-water odors (Persson 1979, 1981, 1983, 1988; Wnorowski 1992; Wnorowski and Scott 1992; Saxby 1993; Jüttner 1995). The FLAVOR Profile (FPA) method was adapted to drinking water by Krasner et al. (1985). The FPA method was also employed by Lin et al. (2002) to determine the odor groups in the source water of two water treatment plants in Taiwan, and chemical analysis showed that MIB and geosmin were present in the source water and were responsible for the musty odor.

MIB and geosmin are stereoisomeric and can be detected easily at low levels by human olfactory senses because of their very low odor threshold concentration

(Cees et al. 1974; Tyler et al. 1978; Persson 1979; Polak and Provasi 1992; Veijanen et al. 1988, 1992; Watson et al. 2000). A Lab test conducted by Jung et al. (2004) revealed that threshold odor levels for MIB and geosmin appeared to be 30 ng/L, which can create consumer complaints. However, concentrations as low as 10 ng/L can impart off-flavors to a variety of food and water sources (Krasner et al. 1985; Dionigi et al. 1993). Concentrations as low as 10 ng/L in water and 0.7 μg/kg in fish can be detected (Zimmerman et al. 2002).

Occurrence of geosmin and MIB are common in aquaculture as bioaccumulation of these sesquiterpenoids in fish and shellfish causes off-flavors in farmed and wild stocks (Persson 1981; Lovell and Broce 1985; Hsieh et al. 1988; Dionigi et al. 1998; Farmer et al. 1995; Lazur 2004). During summer months with higher feeding rates, conditions are conducive to the growth of certain species of algae and bacteria, causing off-flavor in fish and shellfish and making them unmarketable (Kajino and Sakamoto 1995; Eynard et al. 2000). Tellez et al. (2001a) concluded that besides MIB several volatile compounds may cause off-flavor problems in catfish aquaculture; however, off-flavor due to MIB may mask the odors of dimethyl disulfide/trisulfide. Nakajima et al. (1996) and Gagne et al. (1999) reported toxicities levels of geosmin and MIB for sea urchin embryos (*Hemicentrotus pulcherrimus* Agassiz) and rainbow trout (*Oncorhynchus mykiss* Walbaum) (see Table 1).

III Geosmin- and MIB-Producing Species

Geosmin, an earthy-smelling substance, was isolated in 1964 by Gerber and Lechevalier (1965). MIB, a musty- or camphorous-smelling compound, was reported in 1969 by Medsker et al. (1969) and Gerber (1969), and independently by Rosen et al. (1970) in 1970. Geosmin and MIB were first identified in actinomycetes (Gerber 1968, 1969, 1979, 1983; Blevins 1980; Yagi et al. 1981, 1983; Bentley and Meganathan 1981; Schrader and Blevins 1993), then later in cyanobacteria (Izaguirre et al. 1982; Wu and Jüttner 1988; Martin et al. 1991; Matsumuto and Tsuchiya 1988; Tsuchiya et al. 1981; Tsuchiya and Matsumoto 1988; Schrader and Blevins 1993; Tabachek and Yurkowski 1976) and fungi (Kikuchi et al. 1981) that inhabit aquatic and soil environments (Tables 2–4).

Siegmund and Pollinger-Zierler (2006) reported for the first time the presence of *Streptomyces* sp. as the spoilage bacteria of apple juice. Initially, only certain actinomycetes were reported to produce MIB; later, various cyanobacterial species from the genera *Anabaena, Oscillatoria, Lyngbya,* and *Phormidium* have been reported to produce musty and earthy flavors in cultured catfish (Tucker 2000). MIB-producing *Lyngbya* species was reported from Manitoba fish farming (Tabachek and Yurkowski 1976; Yurkowski and Tabachek 1980). In catfish ponds, MIB is usually produced by the blue-green alga *Oscillatoria perornata* (*Planktothrix perornata*) (Tucker 2000). Martin et al. (1988) were the first to report MIB-related off-flavor in commercial farm-raised channel catfish and later attributed it to a planktonic *Oscillatoria* sp. (Martin et al. 1991). Tellez et al. (2001a) reported major

Table 2 MIB-producing species

Species	Origin	Habitat	References
Oscillatoria			
O. perornata (Planktothrix MS988)	Fish pond/USA	Planktonic	van der Ploeg et al. 1995; Tellez et al. 2001a, b; Taylor et al. 2006
O. limosa	Lake/USA	Benthic	Izaguirre and Taylor 1995
Oscillatoria sp.	Fish pond/USA	Planktonic	Martin et al. 1991
O. tenuis	Japan	Planktonic	Negoro et al. 1988
O. geminata	Fish pond/Japan	Fish Pond	Matsumoto and Tsuchiya 1988
O. limnetica	Fish pond/Japan	Fish Pond	Matsumoto and Tsuchiya 1988
Oscillatoria cf. *curviceps*	Lake/USA	Benthic	Izaguirre et al. 1982, 1983
O. tenuis	Water supply/USA	Benthic	Izaguirre et al. 1983
O. variabilis	Fish farming lake/ Japan	Benthic	Tabachek and Yurakowski 1976
O. chalybea	Reservoir/ Israel	Benthic	Leventer and Eren 1970
Phormidium			
Phormidium LP684	Lake/USA	Benthic	Taylor et al. 2006
Phormidium aff. formosum	Water supply/ Australia	Benthic	Baker et al. 2001
P. favosum	Lake/Japan	Benthic	Sugiura et al. 1997
Phormidium	USA	Benthic	Izaguirre 1992
P. tenue	Lake/Japan	Benthic	Sugiura et al. 1986
P. tenue	Water supply/ Japan	Planktonic	Yagi et al. 1983
Pseudanabaena			
Pseudanabaena	Reservoirs/USA	Planktonic	Izaguirre et al. 1999; Taylor et al. 2006
Pseudanabaena	Lake/USA	Planktonic	Izaguirre and Taylor 1998
Other species			
Synechococcus sp.	Water reservoirs/USA	Planktonic	Taylor et al. 2006
Leptolyngbya sp.	Periphyton, lake/USA		Taylor et al. 2006
Lyngbya LO198	Reservoir/USA	Benthic	Taylor et al. 2006
Hyella	Aqueduct water/USA	Epiphytic	Izaguirre and Taylor 1995
Lyngbya Cal.Aq.892	Aqueduct lake/USA	Epiphytic	Izaguirre and Taylor 1995
Planktothrix MS988	Catfish pond/ USA	Planktonic	Martin et al. 1991
Planktothrix cryptovaginata	Fish, water/Finland	Benthic	Persson 1988
Jaaginema geminatum	River/Japan	Benthic	Tsuchiya and Matsumoto 1988
Synechococcus sp.	Plankton, lake/USA	Planktonic	Izaguirre et al. 1984
Lyngbya cf. *aestuarii*	Fish farming lake/ Japan	Benthic	Yurkowski and Tabachek 1980 Tabachek and Yurkowski 1976

Table 3 Geosmin-producing species

Species	Origin	Habitat	References
Anabaena			
Anabaena sp.	Lake/USA	Planktonic	Saadoun et al. 2001
A. laxa CA 783	Lake plankton/USA	Planktonic	Rashash et al. 1996
A. crassa LS698	Lake/USA/Australia	Planktonic	Baker et al. 1994; Komarkova-Legnerova and Cronberg 1992
A. circinalis	River/Australia	Planktonic	Bowmer et al. 1992
A. circinalis	Reservoir/USA	Planktonic	Rosen et al. 1992
A. solitaria	Taiwan	Planktonic	Wu et al. 1991
A. viguieri	Taiwan	Planktonic	Wu et al. 1991
A. macrospora	River/Japan	Planktonic	Tsuchiya and Matsumoto 1988
A. scheremetievi Elenkin	Water supply/USA	Planktonic	Izaguirre et al. 1982
Oscillatoria			
O. limosa	River/Spain	Benthic	Vilalta et al. 2003, 2004
O. limosa	River/Reservoir/ Netherlands		van Breeman et al. 1992
Oscillatoria sp. (Philadelphia)	Periphyton, river/ USA	Benthic	Burlingame et al. 1986
O. brevis	Inland water/Norway	Benthic	Berglind et. al. 1983b
O. simplicissima	Water supply/USA	Pipeline	Izaguirre et al. 1982
O. tenuis	Fish pond/Israel		Aschner et al. 1967
Phormidium			
Phormidium LS1283	Algae, lake/USA	Benthic	Taylor et al. 2006
Phormidium cf. inundatum LO584	Reservoir/USA	Sediment	Taylor et al. 2006
Phormidium sp. (SDC202a,b,c)	Canal/USA		Taylor et al. 2006
Phormidium sp. DCR301	Reservoir/USA	Sediment	Taylor et al. 2006
Phormidium sp. ER0100	Reservoir/USA	Sediment	Taylor et al. 2006
Phormidium DC 699	Algae/lake/USA	Benthic	Taylor et al. 2006
Phormidium sp. LD499	Algae/ lake	Benthic	Taylor et al. 2006
Phormidium sp. LM494	Lake/USA	Sediments	Taylor et al. 2006
Phormidium sp. LS587	Lake/USA	Sediments	Taylor et al. 2006
Phormidium sp. R12	Canal/USA		Taylor et al. 2006
P. allorgei	Lake/Japan	Benthic	Sugiura et al. 1997
Phormidium sp.	Lake/USA	Benthic	Izaguirre and Taylor 1995
P. amoenum	Japan	Benthic	Tsuchiya and Matsumoto 1988
P. simplissimum	Fish, water/Finland	Benthic	Persson 1988
P. formosum	Fish, water/Finland	Benthic	Persson 1988
P. cortianum	Fish farming lake/ Japan	Benthic	Tabachek and Yurakowski 1976
Other geosmin-producing species			
Nostoc sp.	Creek/USA	Periphytic	Taylor et al. 2006
Microcoleus-like cyano	Aqueduct/USA	Epiphytic	Izaguirre and Taylor 1995

(continued)

Table 3 (continued)

Species	Origin	Habitat	References
Lyngbya cf. *subtilis*	Aquaculture pond/ USA	Benthic	Schrader and Blevins 1993
Planktothrix prolifica	Norway	Benthic	Naes et al. 1988
Aphanizomenon gracile	Lake/Germany	Planktonic	Jüttner 1984
Tychonema bornetii	Lake/Norway	Benthic	Berglind et al. 1983a
Schizothrix muellerii	Japan	Benthic	Kikuchi et al. 1973
Symploca muscorum	Fish farming lake/ Japan	Soil	Tabachek and Yurakowski 1976 (first reported by Medsker et al. 1968)
Geitlerenema splendidum	Fish farming lake/ Japan	Benthic	Tabachek and Yurakowski 1976
Actinomycetes			
Streptomyces halstedii	Aquaculture pond/ USA	Sediments	Schrader and Blevins 2001
Streptomyces griseus	USA		Gerber and Lechevalier 1965

Table 4 Geosmin- and MIB-producing species

Species	Origin	Habitat	References
Phormidium			
Phormidium sp. Cal Aq.0100	Aqueduct/USA	Periphyton	Taylor et al. 2006
Phormidium sp.HD798	Algae/lake	Periphytic	Taylor et al. 2006
Phormidium sp.	Lake/USA	Benthic	Izaguirre 1992
Phormidium sp.	River/Japan	Benthic	Matsumuto and Tsuchiya 1988
Phormidium sp.	Inland water/ Norway	Benthic	Berglind et al. 1983b
Other species			
Synechococcus sp CL792	Lake/USA	Planktonic	Taylor et al. 2006
Nostoc sp.	Water treatment plant /Taiwan		Hu and Chiang 1996
T. granulatum	Japan	Benthic	Tsuchiya and Matsumoto 1988
Planktothrix agardhii	Lake/Norway	Planktonic	Persson 1988 Berglind et al. 1983a
O. brevis			Berglind et al. 1983b
Actinomycetes			
Streptomyces	Denmark	Streams/ponds	Klausen et al. 2005
Streptomyces violaceusniger	Water supply/ Jordon	Sediment	Saadoun et al. 1997
Streptomyces sp.	USA		Gerber 1977

volatile compounds such as heptadecane (57%), MIB (29.4%), and benzaldehyde (1.2%) from unialgal continuous cultures of the cyanobacterium *Oscillatoria pernata*. In other environments, many other species of blue-green algae (Tabachek and Yurkowski 1976; Izaguirre et al. 1982; Taylor et al. 2006) and also actinomycetes (Sivonen 1982; Scholler et al. 2002) have been reported to produce MIB. Some of these species also produce toxins (Jardine et al. 1999). Most of the cyanobacteria that produce toxins are planktonic; however, microcystin-producing benthic cyanobacteria have also been reported (Izaguirre et al. 2007), which have been characterized by 16S rRNA technique. Off-flavors other than musty and earthy in catfish are woody and pine and have been attributed to the presence of unspecific cyanobacteria (van der Ploeg 1991).

Izaguirre and Taylor (2004) observed, in drinking water supplies in the U.S., that known geosmin-and MIB-producing cyanobacteria belong to genera such as *Anabaena*, *Oscillatoria*, *Phormidium*, *Lyngbya*, *Leptolyngbya*, *Microcoleus*, *Nostoc*, *Planktothrix*, *Pseudanabaena*, *Hyella*, *and Synechococcus* (see Tables 2–4). Many MIB- and geosmin-producing *Oscillatoria* strains have been isolated from water supplies in California (Izaguirre et al. 1982).

Cultures of two *Oscillatoria* strains isolated from drinking water reservoirs in California produced 60–150 μg/L MIB (Izaguirre et al. 1982). Cultures of *O. geminata* and *O. limnetica* isolated from a fish cultivation pond and a park pond in the Tokyo area produced 550 and 240 μg/L MIB, respectively (Matsumoto and Tsuchiya 1988). *Phormidium tenue*, a major cause of MIB episodes in Lake Biwa (Yagi et al. 1983) and Lake Kasumigaura, Japan (Sugiura et al. 1986, 1998), produced 120 μg/L MIB in culture (Negoro et al. 1988). *O. limnetica* is considered synonymous with *Pseudanabaena limnetica* (Anagnostidis and Komárek 1988; Baker 1992). Two MIB-producing (240–260 μg/L) cyanobacteria, *Lyngbya* strains, were isolated from a major aqueduct system in California (Izaguirre and Taylor 1995). *Lyngbya* was a comparatively strong MIB-producing species relative to other MIB producers (Martin et al. 1991; Izaguirre 1992).

Planktonic and benthic species synthesize both compounds, geosmin and MIB (see Tables 2–4). The first planktonic MIB producers were reported in Japan (Yagi et al. 1983; Negoro et al. 1988) and later in Australia (Baker et al. 1994). The first major planktonic MIB producer isolated in the U.S. was the planktonic *Oscillatoria* (*Planktothrix*) from a catfish pond in Mississippi (Martin et al. 1991). Some new strains of *Pseudanabaena* species isolated from Castic Lake, California, represented the major planktonic MIB producers isolated from drinking water in the U.S. (Izaguirre and Taylor 1998).

Izaguirre and Taylor (2004) noted that some MIB-producing cyanobacteria isolated in the U.S. have morphological analogues in other parts of the world. MIB-producing *Planktothrix* sp. (originally called *Oscillatoria*) isolated from a catfish pond in Mississippi (Martin et al. 1991; van der Ploeg et al. 1995) appears indistinguishable from an MIB-producing *Planktothrix* species in Australia (Baker 1992), and may also be related to an *Oscillatoria* cf. *raciborskii* reported in Japan (Hosaka et al. 1995), and possibly also to the *O. tenuis* reported by Negoro et al. (1988). The other example is MIB-producing *Pseudanabaena* (Izaguirre and Taylor 1998; Izaguirre et al. 1999), some strains of which are morphologically similar to the MIB producer *Phormidium tenue* in Japan, reported by Yagi et al. (1983). Izaguirre and Taylor (2004) observed that *Pseudanabaena* strains isolated in the U.S. may also be related to the MIB-producing strain of *Oscillatoria limnetica* reported by Matsumoto and Tsuchiya (1988), as this species is considered synonymous with *Pseudanabaena limnetica* by Anagnostidis and Komárek (1988) and Baker (1992).

The first reports of geosmin production by *Anabaena circinalis, Anabaena laxa*, and *Symploca muscorum* were published by Henley (1970), Rashash et al. (1996), and Medsker et al. (1968), respectively. Many species of blue-green algae and actinomycetes can produce geosmin, but in catfish ponds, the main geosmin producers are species of the blue-green alga *Anabaena*, followed by *Aphanizomenon* or *Lyngbya* (van der Ploeg et al. 1992; Schrader and Blevins 1993). A geosmin-producing *Oscillatoria* strain and one *Anabaena* species were isolated from drinking water supplies in California (Izaguirre et al. 1982). Geosmin- and MIB-producing cyanobacteria found in the U.S. also occur in other countries. In Australia, *Anabaena circinalis*, which produces geosmin along with saxitoxin, is a major problem, causing the deaths of animals (Negri et al. 1995). This species is also reported from South African reservoirs (Wnorowski and Scott 1992). *Oscillatoria splendida* (now called *Geitlerinema splendidum*) is a common geosmin producer widespread throughout the Northern Hemisphere.

Nielsen et al. (2006) found that bacterial groups within *Actinobacteria* produce the compounds geosmin and MIB, which lower the quality of surface water when used for drinking. Results indicate that combined microautoradiography and catalyzed reporter deposition (CARD-FISH) may serve as an effective tool when studying identity and activity of microorganisms within freshwater environments (Nielsen et al. 2006). Klausen et al. (2005) attributed the occurrence of the geosmin and MIB in freshwater environments to *Actinobacteria,* most of them belonging to the genus *Streptomyces* (Schrader and Blevins 1993; Zaitlin et al. 2003; Zaitlin and Watson 2006). The new species *Penicillium discolor*, frequently isolated from nuts, vegetables and cheese, also produces the moldy-smelling compounds geosmin and MIB (Frisvad et al. 1997). A correlation between the occurrence of geosmin, argosmin and heptadec-*cis*-5-ene and the presence of the cyanobacterium *Aphanizomenon gracile* was observed by Jüttner (1984). These compounds were present in spring and autumn, when *A. gracile* also occurred in the lake, but were not detected in summer, when the organism was absent.

A *Phormidium* sp. reported by Izaguirre (1992) was rare among cyanobacteria in that it could produce both MIB and geosmin (see Table 4). Five other cyanobacteria with this property have been reported: three strains in Norway (Berglind et al. 1983b), one in Japan (Matsumoto and Tsuchiya 1988), and one in Taiwan (Wu and Jüttner 1988). Schrader and Dennis (2005) reported that geosmin and MIB were implicated for earthy and musty off-flavors, respectively, in farm-raised channel catfish (*Ictalurus punctatus*) in the Southeastern U.S. MIB-producing cyanobacterium (*Oscillatoria perornata*) is present in catfish ponds in both Mississippi and Alabama Blackland Prairie (MABP), whereas geosmin was found to be more prevalent in catfish ponds in the MABP region than West Mississippi.

IV Biosynthesis of Geosmin

Bentley and Meganathan (1981) used radiogas chromatography to investigate biosynthesis of geosmin, the characteristic odoriferous constituent of *Streptomyces* species. Based on the incorporation of acetate into geosmin by strains of *S. antibioticus*, they concluded that geosmin was likely a degraded sesquiterpene. Actinomycetes, gram-positive soil bacteria *Streptomyces avermitilis* and *S. coelicolor*, produce geosmin, and germacradienol has been identified as a precursor/cometabolite of geosmin in streptomycetes and myxobacteria (Cane and Watt 2003). The *S. avermitilis* gene SAV 2163 (geoA) and *S. coelicolor* A3 (2) SCO6073 gene encodes germacradienol/geosmin synthase (Jiang et al. 2006; Gust et al. 2003). Among the sesquiterpene synthases, the 2178-bp geoA gene (SAV 2163) encodes a putative protein of 725 amino acids with a significant similarity to the *S. coelicolor* A3(2) SCO6073 2181-bp gene product encoding 726 amino acids (Gust et al. 2003; Cane and Watt 2003). Deletion of the entire SCO6073 (SC9B1.20) gene from *S. coelicolor* A3(2) results in complete loss of geosmin production (Cane and Watt 2003; Gust et al. 2003); this provides evidence that SCO6073 encodes a germacradienol synthase, which catalyzes an essential step in the biosynthesis of geosmin. *Streptomyces avermitilis* mutants with a deleted geoA were unable to produce either germacradienol or geosmin, and biosynthesis of both compounds was restored by introducing intact geoA gene in mutants (Cane et al. 2006).

Cane and Watt (2003) expressed a 2181-bp gene from *S. coelicolor* A3(2) (SCO6703 = SC9B1.20) in *Escherichia coli* to give a 726-amino-acid protein and originally proposed that formation of geosmin from germacradienol would involve multistep biochemical redox pathways catalyzed by several hypothetical enzymes, which has also been suggested by other researchers (Spiteller et al. 2002; Dickschat et al. 2005). Cane and Watt (2003) and He and Cane (2004) revealed that biosynthetic conversion of fernesyl diphosphate to geosmin requires a divalent cation, preferably Mg^{2+} and no other organic or inorganic cofactor is required. Recently, Jiang et al. (2006) successfully demonstrated that a single enzyme (germacradienol D synthase) is both necessary and sufficient to catalyze biosynthesis of geosmin from fernesyl diphosphate without requirement of any additional enzymes and redox cofactors, which solved the long-standing biosynthetic mystery.

Farnesol (3,7,11-trimethyl-2,6,10-dodecatrien-1-ol) is considered the universal precursor of the sesquiterpenes (Croteau 1987). Studies conducted by Dionigi et al. (1991) on the effect of farnesol on the growth and metabolism of the geosmin-producing actinomycete *Streptomyces tendeae* revealed that farnesol can inhibit geosmin synthesis, which in turn suppresses geosmin-producing species.

V Remediation of Off-Flavors

A Conventional Physical Methods

Management strategies for muddy and musty off-flavors are limited as geosmin and MIB are recalcitrant to conventional water treatment (Ho et al. 2007). However, some conventional physical techniques have been recommended. These sesquiterpenoids degrade over time and are purged from the fish, depending on their concentrations, water temperature, and water quality (Tucker and van der Ploeg 1999).

The minimum period required for fish to regain flavor quality is the cause of concern for aquaculturists (Dionigi et al. 2000). Lazur (2004) observed that holding fish in raceways with flow-through well water can purge geosmin and MIB off-flavors from fish; however, this process involves additional costs from harvesting and handling, tank facility overhead, water pumping, requirement of large amount of water (Johnsen and Dionigi 1993) and fish weight loss and mortality. Purging recirculating systems may be more practical but biological filters and other components of systems may become off-flavor sources (Johnsen and Dionigi 1993). van Breeman et al. (1991) reported an effective and environmentally friendly technique for the control T/O problems caused by algal activity in a reservoir, where sediment surface was disturbed with a harrow pulled by a boat.

Uptake and depuration of MIB from fish are important considerations in the design and implementation of systems to remove off-flavors from fish before processing (Johnsen et al. 1996). Flavor can be evaluated by tasting and assigning grades when fish is cooked in a microwave; flavor from a distinct to slight off-flavor is indicative of clearing of flavor, and the fish may soon be marketable (Lazur 2004). Song and O'Shea (2007) reported degradation of geosmin and MIB through ultrasonic irradiation, which may have potential applications in the removal of T/O compounds from potable water supplies and fish farms.

B Chemical Methods

Blue-green algae can be eliminated to some extent by chemical use in ponds (Wagner et al. 1999). One of the management practices to prevent or kill the growth of unwanted cyanobacteria includes the application of algicides to fish ponds (Tucker and van der Ploeg 1999; Lazur 2004). Copper sulfate, chelated-copper compounds, and diuron (3-[3,4-dichlorophenyl]-1,1-dimethylurea) are the USEPA-approved compounds for use in catfish production ponds as algicides (Schrader et al. 1998a,b, 2003; Schrader and Harries 2001; Tucker and Leard 1999). Most of the cyanobacteria are sensitive to 1–2 mg/L cupric ion, and some of them are affected even at 5 µg/L (Horne and Goldman 1974). An *Oscillatoria* species isolated in India was damaged at 1 mg/L copper sulfate after 8 d and failed to grow when transferred to growth medium (Arora and Gupta 1983). Studies conducted by Schrader and Blevins (2001) on the testing of trace elements revealed that copper had the most inhibitory effect on biomass and geosmin production at a concentration as low as 10.7 µM, and it was concluded that copper applied in the form of copper sulfate to the sediments of drained fish ponds might help prevent future off-flavor occurrences.

Prolonged use of copper sulfate can result in accumulation in the sediments, as shown in the Fairmont Lakes in Minnesota (Hanson and Stefan 1984) and Lake Monona, Wisconsin (Nichols et al. 1946). Large quantities of gesomin and MIB are retained in the blue-green cells, which may rupture on copper sulfate application with the result of rapid release of these intracellular odorous compounds (Negoro et al. 1988; Wu and Juttner 1988; Bowmer et al. 1992; Martin et al. 1991; Rosen et al. 1992; Utkilen and Frøshaug 1992). In Live Oak reservoir, Southern California, geosmin levels increased from 34 to 150 ng/L on copper sulfate application for control of geosmin-producing cyanobacteria.

The copper dose required to control a particular alga is not always effective because of its temporary effects (Izaguirre and Devall 1995) and the higher dose requirement, especially in alkaline waters, wherein it precipitates. Copper used for algal control has been found to be toxic to various freshwater fish, and speciation has a potential role in the toxicity of copper. It has been found that its continued use can result in copper-tolerant algal strains, requiring even higher doses for control (Izaguirre and Devall 1995), as evidenced in Lake Norrviken in Sweden (Ahlgren 1970), the Fairmont Lakes in Minnesota (Moyle 1949; Hanson and Stefan 1984), Mill Pond Reservoir in Massachusetts (McKnight et al. 1982), and Canadian prairie dugouts or farm ponds (Peterson and Swanson 1988). In Canada, continued application of copper sulfate favored the growth of *Oscillatoria* (Klassen et al. 1970). Copper tolerance has also been reported in various algae in lakes in Ontario, Canada (Stokes et al. 1973; Butler et al. 1980) and a river in England (Foster 1977).

Lyngbya, *Nostoc*, *and Phormidium* have been reported as copper-resistant blue-green algae (Palmer 1977). Izaguirre (1992) isolated a copper-tolerant benthic *Phormidium* sp., which produces MIB in Lake Mathews, California. The release of MIB in this reservoir has been linked with a cyanobacterium, *Oscillatoria curviceps*, first found in 1978 by Izaguirre et al. (1982). Later, by 1989, *Phormidium* had appeared all around the reservoir, following the decline of *O. curviceps*, which indicates that eradication of one taste-and-odor producer can be followed by the proliferation of another undesirable organism (Izaguirre 1992). The tolerance of *Phormidium* up to 3.5 mg/L copper in culture has been attributed to the repeated use of copper sulfate in the reservoir. Zimba et al. (2002) found that weekly applications of diuron to catfish ponds altered the taxonomic composition of the phytoplankton communities as the filamentous cyanobacteria were replaced by coccoid cyanobacteria. A copper-resistant strain of *M. aeruginosa* has been discovered by Garcia-Villada et al. (2004).

It has been observed (Izaguirre and Devall 1995; Tucker 2000; Han et al. 2001; Boylan 2001; Schrader et al. 2003; Tung et al. 2004) that synthetic algicides have the following adverse impacts: (i) toxicity toward phytoplankton that can lead to the death of the entire phytoplankton community and subsequent water quality deterioration; (ii) persistence in the environment; (iii) the public's negative perception of the use of synthetic herbicides in food fish production ponds; (iv) environmental safety issues from copper accumulation in the pond sediments; (v) adverse affect on microbial activity in pond sediments from long-term applications; (vi) deterioration of water quality resulting in the need for more aeration; (vii) pH fluctuation; (viii) dissolved oxygen depletion; and (ix) additional costs from multiple treatments as algae can reestablish in nutrient-rich water.

Studies conducted by Tung et al. (2004) on the effect of three different oxidants on MIB concentration in the presence of cyanobacteria in raw water revealed that ozonation was the most effective technique for the removal of both MIB and geosmin. Glaze et al. (1990) reported similar results in which 80%–90% of geosmin and MIB were removed by treatment with ozone. Ozonation appeared to affect the MIB concentrations by releasing it from damaged cells and oxidizing soluble MIB (Tung et al. 2004). Ozonation followed by biological filtration has the potential to provide effective treatment, as shown by Elhadi et al. (2004) in bench-scale experiments using granular activated carbon and sand for the removal of geosmin and MIB. Persson et al. (2007) used biofiltration to investigate differences between adsorption and biodegradation. They suppressed microbial activity by adding azide in granular activated carbon crushed in expanded clay. It was found that granular activated carbon still removed gesomin and MIB nearly unaffectedly, whereas in the clay biofilter, removal of both odorants ceased completely. Other oxidation processes using chlorine, chloramines, and potassium permanganate are ineffective for reducing geosmin and MIB as these oxidants cause only cell damage and the release of intracellular MIB into the water (Tung et al. 2004). These results are similar to those of Glaze et al. (1990). Peterson et al. (1995) also found that chlorine and permanganate caused extensive damage to algal cells, inducing the release of geosmin and dissolved organic carbon. Ashitani et al. (1988) observed an increase of MIB and geosmin concentrations in water following prechlorination at a water treatment plant. Jung et al. (2004) studied removal of geosmin and MIB by oxidation (O_3, Cl_2, ClO_2) and adsorption. They observed higher removal efficiency with increased ozone dosage and, in the case of pulverized activated carbon, adsorption efficiency of geosmin was superior to MIB. As an alternative to these synthetic algicides, natural compounds and extracts from plants are being screened for use in catfish aquaculture (Schrader et al. 2003; Meepagala et al. 2005).

C Environmentally Safe Plant-Derived Algicides

The discovery of eco-friendly, selective algicides that suppress the growth of the cyanobacteria implicated in musty off-flavor in pond-cultured catfish would be beneficial for the aquaculture industry. Green algae do not produce such undesirable odors, are good oxygenators of the water, and form a base for periphytic food growth in catfish production (Paerl and Tucker 1995); thus, the discovery of safe selective compounds that kill cyanobacteria would be beneficial for the aquaculture industry. Previous research (Schrader and Harries 2001; Schrader et al. 1998a,b) has identified several natural compounds that are selectively toxic toward *O. perornata*. 9,10-Anthraquinone, found in plant tannin extracts (Robinson 1967), has a high degree of selective toxicity toward *O. perornata* (Schrader et al. 1998a, b) and also inhibits its photosynthesis (Schrader et al. 2000). Previous studies shows that in comparison with copper-based products and diuron (half-life, 2 wk in pond water), anthraquinone-59 derived from the natural compound 9,10-anthraquinone has much lower persistence in pond water (half-life 19 hr) and also has greater selective toxicity toward cyanobacteria than other phytoplankton (Tucker 2000). In addition, the application of anthraquinone-59 in food fish production is advantageous in view of the public's negative perception of diuron.

Meepagala et al. (2005) extracted rutacridone epoxide from *Ruta graveolens* roots, which has potent selective algicidal activity toward the MIB-producing blue-green alga *Oscillatoria perornata*. Rutacridone epoxide is reported as a direct-acting mutagen, precluding its use as an agrochemical, and none of the synthetic analogues showed comparable activities to rutacridone epoxide (Meepagala et al. 2005). Many *Ruta* species are sources of diverse classes of natural products with biological activity including antifungal, phytotoxic, and antidotal (de Feo et al. 2002; Oliva et al. 2003). Oliva et al. (2003) demonstrated the presence of fungicidal constituents in the ethyl acetate extract of *Ruta graveolens* L. leaves against some agriculturally important fungi.

Tellez et al. (2001b) screened *F. cernua* extracts against two species of cyanobacteria and one species of green algae to determine their potential as a selective cyanobactericide. They found that the ether extract of *F. cernua* was selectively inhibitory against the cyanobacterium responsible for the MIB induced off-flavor associated with catfish farming operations.

D Lignocellulosic Agrowastes: Inexpensive Biosorbents

Activated carbon has been used very frequently for the removal of geosmin and MIB from natural water (Hung and Lin 2006), raw water (Cook et al. 2001), and drinking water (Hepplewhite et al. 2004; Elhadi et al. 2004; Liang et al. 2005). Nowack et al. (2004) investigated methods for tailoring a commercial, lignite-based granular activated carbon to enhance its adsorption of MIB from natural water. Cook et al. (2001) reported that powdered activated carbon (PAC) can effectively remove MIB and geosmin when the correct dose is applied, especially where a higher dose is required in the case of very turbid water. The high cost of activated carbon restricts its large-scale use for abatement of these metabolites, and in recent years the search for low-cost adsorbents has grown. By-products of lignocellulosic agroindustrial production have been studied for potential use as inexpensive biosorbents (Ng et al. 2002a, b). Barley straw inhibits the growth of cyanobacteria blooms (Barrett et al. 1996; Caffrey and Monahan 1999; Ferrier et al. 2005), which has been attributed to the antialgal activity of phenolics (tannins) present in the straw (Pillinger et al. 1994). Lignocellulosic materials have the advantage of being readily available because the world's industry utilizes less than 10% of raw material biomass from plantations (Pauli and Gravitis 1997). The remainder is waiting for effective utilization and could provide value-added products. Many other applications for these residues are in the process of being developed. Development of cost-effective and environment-friendly products from agricultural wastes/by-products and plantations for the aquatic bioremedition of brackishwater aquaculture is the objective of continued research of Central Institute of Brackishwater Aquaculture, Chennai, India (Krishnani et al. 2002, 2003, 2004, 2005, 2006b, 2006c; Krishnani and Ayyappan 2006; Parimala et al. 2004, 2007).

E Bioremediation

Microbes metabolize a broad range of aquatic pollutants by complex enzyme-catalyzed reactions. The genes encoding these proteins are localized on either large catabolic plasmids or the genomic DNA. Horizontal transfer of genes among bacteria has a major impact on the adaptability of bacteria during changing environmental conditions (Trevors et al. 1987). Gene bioaugmentation is the process of obtaining enhanced activity after gene transfer from an introduced donor organism into a member of the indigenous microbial environment (Pepper et al. 2002). This process has the potential to become a powerful tool in environmental management (DiGiovanni et al. 1996; Chen and Wilson 1997; Grommen and Verstraete 2002; Debashish et al. 2005).

To date, investigations related to bioremediation of geosmin and MIB are limited. Both are major causes of concern because they are difficult to remove by conventional water treatment methods (Lalezary et al. 1986). Biodegradation could be an alternative remediation technique, which needs to be investigated. Izaguirre et al. (1988) isolated mixed bacterial populations that biodegrade MIB slowly at ppb levels, whereas the related naturally occurring compound isoborneol was degraded rapidly, even at ppm levels, which may be attributed to the absence of the methyl group at carbon 2 in isoborneol and its presence in MIB, which might exert steric hindrance of the hydroxyl group (Medsker et al. 1969; Trudgill 1984).

Saadoun (2005) studied the ability of *Pseudomonas* sp. isolated from different soils contaminated with fuel spills to degrade MIB. The *Pseudomonas* group, especially *P. aeruginosa*, is common in freshwater and sediments (Hoadley 1968; Pellett et al. 1983) and well known for its metabolic versatility resulting from utilization of a wide range of substrates (Stainer et al. 1966). However, it has been reported that natural strains of this species do not have plasmids that encode degradative genes (Haas 1983). Walker and Higginbotham (2000) isolated an aquatic bacterium from pond water that could be a potential microbial algicide to lyse cells of some selected cyanobacteria, including species of *Anabaena* and *Oscillatoria*. Studies conducted by Klausen et al. (2005) showed that indigenous stream bacteria were capable of reducing the odors caused by geosmin and MIB produced by *Streptomyces*, and that enrichment with Luria-Bertani medium stimulated the degradation.

Lauderdale et al. (2004) isolated and characterized a bacterium implicated in aerobic degradation of MIB. Its 16S-rRNA phylogenetic analysis revealed that it is more closely related to *Bacillus fusiformis* and *Bacillus sphaericus*. Westerhoff et al. (2005) observed a magnitude change in MIB concentrations caused by thermal destratification of the reservoirs and concluded that biodegradation appeared more important than volatilization, photolysis, or adsorption. Saadoun (2005) modified the method of Jacobs et al. (1983) to determine the ability of different *Pseudomonas* sp. to degrade MIB-like compounds by transforming them to alcohol, detection of which would be an applicable approach for detecting the activity of microorganisms on this volatile compound.

Saadoun and El-Migdadi (1998) suggested that naturally occurring geosmin produced by *Streptomyces halstedii* could be degraded by specific species of gram-positive bacteria. They applied the technique of detection of alcohol production as a result of odorous compound oxidation for the screening of bacteria that degrade geosmin-like compounds. Hoefel et al. (2006) reported the cooperative degradation of geosmin by a consortium comprising three gram-negative bacteria isolated from a biologically active sand filter column, similar to cultured species such as *Sphingopyxis alaskensis*, *Novosphingobium stygiae*, and *Pseudomonas veronii*. They also observed that none of these three isolates was shown to be capable of degrading geosmin either individually or in any combination of two. Yagi et al. (1988) reported the degradation of more than 50% of geosmin and MIB adsorbed onto a bioactivated carbon filter seeded with *Bacillus subtilis*. Ho et al. (2007) reported biological sand filtration as an effective process for the biodegradation of MIB and geosmin, followed by batch bioreactor using biofilm. They identified a *Pseudomonas* sp., *Alphaproteobacterium*, *Sphingomonas* sp., and an *Acidobacteriaceae* member most likely involved in the biodegradation of geosmin.

Summary

Microbially derived off-flavors can adversely affect the beverage, food, water, and aquaculture industries. Off-flavor can temporarily be controlled by adopting best management practices such as proper aeration, liming, and dredging, and, more importantly, by avoidance of excessive nutrient use. Research studies focus on the effective means of control with the major emphasis on controlling the odor-causing algae populations and developing effective and selective algicides, which are not always available for use at the right time and can also have adverse impacts on the environment. Furthermore, selective application of synthetic algicides is not always recommended for reasons of inconsistency in the results and concerns regarding the frequent use of these chemicals, such as toxicity, accumulation of free copper, dissolved oxygen voids, increase in toxic ammonia and hydrogen sulfide, pH fluctuation, reduced photosynthetic activity, and reestablishment of algae in nutrient-rich water, thus requiring multiple treatments. Conversely, the plant-derived products appear to be environmentally safe and economical in view of their abundant availability and easy operational process. However, there needs to be more extensive work in this field. Precursors of sesquiterpene synthesis may selectively help to suppress off-flavor-producing species. Bioremedial measures by means of microbial degradation and gene bioaugmentation may be promising and are the subjects of much future research for effective controls.

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