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Chapter 20

Harmful Algal Blooms

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I. INTRODUCTION AND OVERVIEW

(S. Watson and J. Wehr)

Harmful algal blooms (HABs) are a major issue in marine, brackish, and freshwater systems worldwide (Hallegraeff, 1993). Algal blooms are not a new phenomenon and occur naturally in fertile regions (such as the North American prairies), with historical accounts of these outbreaks dating back at least two millennia (Carmichael, 2008). However, with the increasing environmental degradation over the past century there has a dramatic rise in the severity and geographical range of these events across large and small lakes, reservoirs, rivers, ponds, dugouts, and a wide range of other surface waters throughout the world. Severe and often prolonged HABs now plague some of the world's largest waterbodies, such as Lakes Erie, Ontario, Okeechobee, and Winnipeg (North America; Fig. 1), Taihu (China), Kasumigaura (Japan), Kinneret (Israel), Victoria (Africa), and the Baltic and Caspian Seas (Europe and West Asia, respectively) (Paerl and Paul 2011; Kling et al., 2011; Zohary et al., 2012).

HABs are symptomatic of ecosystem imbalance, often caused by the many environmental changes that manifest the expanding global human footprint and climate change. These changes fall under three general categories: (a) watershed development, including land development, deforestation, damming and rerouting of rivers; this can modify water channels, volume and flushing, and the timing and levels of material inputs to surface waters (i.e., nutrients, sediment, and other pollutants); (b) climate-related changes, affecting ice cover and the length of the growing season, timing and magnitude of hydrologic events (e.g., more frequent severe storms, flooding, higher spring runoff, extended periods of low or no inflow), water temperature, in-lake mixing and circulation patterns, and transport of dissolved and particulate materials; and (c) biological changes, affecting the consumption, integrity, and viability of cyanobacterial cells (e.g., aquatic invasive species, AIS) (Fig. 2). HABs are typically more severe and frequent in eutrophic and mesoeutrophic waters, but they also occur intermittently in less productive systems, particularly those with some degree of human impact such as acidification, organic loading, or history of restorative nutrient reduction (Nicholls et al., 1982; Watson et al., 1999; Søndergaard et al., 2007; Noges et al., 2010; Carey et al., 2012; Francis et al., 2014).
Bloom events exemplify the remarkable capacity of algae and cyanobacteria to exploit and engineer habitats to their advantage, presenting an ever-evolving challenge to scientists and managers (e.g., Duarte et al., 2009; Mehnert et al., 2010; Aubriot and Bonilla, 2012). Public awareness and concern with HABs has escalated in recent decades, and the term harmful bloom is often used indiscriminately in both scientific and popular media. In fact, “algal bloom” is not a defined or quantitative measure, but is used in a general sense to describe a visible development of planktonic or attached algae. Harmful blooms are differentiated from other blooms as those that have detrimental ecological, public health, and/or socioeconomic impacts.

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FIGURE 1 Cyanobacterial blooms. (A) Lake Erie during a bloom composed mainly of Microcystis spp., on March 22, 2014, viewed from space. (B) Surface bloom of Microcystis in Hamilton Harbor, western Lake Ontario. (C) Microscopic appearance of Microcystis aeruginosa. (D) Lake Winnipeg during a summer bloom of Aphanizomenon sp. (E) Surface appearance of Aphanizomenon in Lake Winnipeg. (F) In a backwater on the upper Mississippi River. (G) Microscopic appearance of Aphanizomenon cf. flos-aquae. (H) Accumulation of Lyngbya wollei mats along the shore Maumee Bay (Ohio), Lake Erie. (I) Rake-sampling Lyngbya wollei from Lake Mahopac, New York. (J) Microscopic appearance of Lyngbya wollei.
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Release of nutrients, metals, and toxic gases (H$_2$S, NH$_3$, CH$_4$) and negative impacts on invertebrates, fish, and other aerobes. Freshwater HABs and eutrophication in the United States alone were estimated to cost about $2-4 billion in 2004 in industrial losses, monitoring, management, and mitigation (Dodds et al., 2009; Hudnell, 2008, 2010; Steffensen, 2008). Blooms are often comprised of species that are inedible or low in nutritional quality to invertebrate grazers, negatively affecting foodweb biodiversity and production (Huisman et al., 2005; Paerl and Otten, 2013).

Relatively few freshwater HAB species produce human toxins—and all of those known to date are cyanobacteria (fewer than 50). However, the actual number of toxic species is likely underestimated, because the capacity to produce toxins varies both among species and strains of the same species and/or with environmental conditions; furthermore, the majority have not been tested or identified to species level (Bláha et al., 2009; Quiblier et al., 2012). On the other hand, a far wider range of HAB taxa (both prokaryotes and eukaryotes) produce many other bioactive compounds (semiochemicals), many of which are harmful to other organisms (allelogenic) such as metabolic, protease, and chitinase inhibitors, teratogens, bleaching agents, antibiotics, and carcinogens. Individual blooms may produce a variety of these semiochemicals (together or in succession), which act synergistically and/or target different organisms or life stages (see Section IV, Chemical Ecology).

HAB species include representatives from most major taxonomic groups (Hallegraeff, 1993). Nevertheless, despite this diversity, many HAB taxa respond to similar broad environmental stimuli (e.g., nutrients, light, temperature) and employ similar growth and defense strategies to allow them to maximize growth and minimize losses (Table 1). In inland waters, attention is often focused on dense surface HABs caused by planktonic cyanobacteria (“cyanoHABs” or “cHABs”), and the past few decades have seen an apparent increase in cHAB frequency and geographical range (Carmichael, 2008; Winter et al., 2011; Elliott, 2012; Deng et al., 2014). There has also been an apparent rise in blooms of eukaryotic phytoplankton, including some recently invasive flagellates (Watson et al., 2001a,b; Paterson et al., 2008; Auer et al., 2010; Roelke et al., 2011; Trigal et al., 2013). Reports of thick shoreline and benthic mats of chlorophytes, cyanobacteria, and other benthic HABs are likewise increasing (Fig. 1H–J; Joyner et al., 2008; Hudon et al., 2014; Section III, Benthic HABs).

Research has made tremendous advances in our understanding of HAB events, yet they remain poorly understood. Here we aim to provide an overview of these intriguing and challenging phenomena that affect ecosystems and human society. While HABs are as diverse as the water bodies they affect, we focus on some specific examples of known HAB taxa that affect inland waters in North America and highlight some of the important strategies used by these species to enable their excessive growth. The evolving taxonomic classification of many of these taxa has led to inconsistencies among recent and older reports. For this reason, current names are used here, with reference to older names used in past reports.

**FIGURE 2** Conceptual diagram illustrating external and internal factors controlling growth, accumulation (as blooms), and fate of cHABs in freshwater ecosystems. Factors can act individually or in combined (synergistic, antagonistic) ways.
### TABLE 1 HABs: Examples of Major HAB Taxa, Impairments, and Adaptations Enabling Species Dominance and Proliferation

<table>
<thead>
<tr>
<th>Taxonomic Group</th>
<th>CYAN</th>
<th>CHLOR</th>
<th>DIAT</th>
<th>CHRYS</th>
<th>EUG</th>
<th>RHAPH</th>
<th>HAPT</th>
<th>DINO</th>
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<tbody>
<tr>
<td>Major HAB taxa</td>
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<tr>
<td>planktonic (P);</td>
<td>Anabaena (P), Microcystis (P)</td>
<td>Cladophora (B)</td>
<td>Aulacoseira (P)</td>
<td>Uroglena (P)</td>
<td>Euglena (P)</td>
<td>Prymnesium (P)</td>
<td>Ceratium (P)</td>
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<tr>
<td>benthic (B)</td>
<td>Aphanizomenon (P)</td>
<td>Spirogyra (P,B)</td>
<td>Cyclatella (P)</td>
<td>Dinobryon (P)</td>
<td>Conostomum (P)</td>
<td>Chrysochromulina (P)</td>
<td>Peridinium (P)</td>
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<tr>
<td></td>
<td>Planktothrix (P)</td>
<td>Mougeotia (P,B)</td>
<td>Stephanodiscus (P)</td>
<td>Chrysosphaerella (P), Synura (P)</td>
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<td></td>
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<td></td>
<td>Cylindrospermopsis (P)</td>
<td>Hydrodictyon (P,B)</td>
<td>Didymosphenia (B)</td>
<td>Mallomonas (P)</td>
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<tr>
<td></td>
<td>Cloeotrichia (P,B)</td>
<td>Lyngbya (B)</td>
<td></td>
<td>Hydrurus (B)</td>
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<td></td>
<td>Lyngbya (B)</td>
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<tr>
<td>Major impairments</td>
<td>Toxins (H, F), allelogens, irritants, carcinogens; T&amp;O (D, I), shading, occlusion, fouling, hypoxia, reduced biodiversity</td>
<td>T&amp;O (I), toxins (F), allelogens, teratogens, hypoxia, shading/occlusion; reduced biodiversity</td>
<td>T&amp;O (D,I), toxins (F), allelogens, reduced biodiversity</td>
<td>Toxins (F), allelogens</td>
<td>Irritants, T&amp;O (D,I), allelogens, reduced biodiversity</td>
<td>T&amp;O (D,I), toxins (F), allelogens, reduced biodiversity</td>
<td>T&amp;O (D), allelogens, reduced biodiversity</td>
<td></td>
</tr>
<tr>
<td>Adaptations to maximize growth: resource acquisition/exploitation/storage (low/high/pulsed supplies); reproduction/propagation/dispersal</td>
<td>“Luxury” uptake; SAV (mucilage/hairs, shape), APAses/DOP (e.g., phosphonate) poly-P bodies; motility (B)</td>
<td>SAV (mucilage/hairs, shape), APAses/DOP, motility</td>
<td>Low P uptake; SAV (mucilage, stalks) DOP, motility (B)</td>
<td>Low P uptake; SAV DOP, motility, phagotrophy</td>
<td>DOP, SAV, motility, phagotrophy</td>
<td>Low-P; acid phosphatase</td>
<td>Motility, phagotrophy</td>
<td></td>
</tr>
<tr>
<td>Phosphorus</td>
<td>NA</td>
<td></td>
<td>M</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nitrogen</td>
<td>N₂ fixation (via heterocytes/cell compartmentalization); DON (urea etc); cell storage</td>
<td>SAV; mucilage/hairs, shape, motility</td>
<td>SAV; motility(benthic)</td>
<td>SAV; motility, phagotrophy</td>
<td>SAV; motility, phagotrophy</td>
<td>ND</td>
<td>Motility, phagotrophy</td>
<td>Motility, phagotrophy</td>
</tr>
<tr>
<td>Carbon</td>
<td>CCMS, DOC; heterotrophy (SO₄ reduction), motility (B); cell storage</td>
<td>CCMs; DOC; cell storage</td>
<td>DOC; motility (benthic); cell storage</td>
<td>DOC; motility, phagotrophy; cell storage</td>
<td>DOC; motility; cell storage</td>
<td>DOC; motility; phagotrophy; cell storage</td>
<td>DOC; motility; phagotrophy; cell storage</td>
<td>DOC; motility; phagotrophy; cell storage</td>
</tr>
<tr>
<td>Trace metal/elements</td>
<td>Siderophores</td>
<td>Siderophores</td>
<td>Phagotrophy</td>
<td>Phagotrophy</td>
<td>Phagotrophy</td>
<td>Selenium; phagotrophy</td>
<td>Phagotrophy</td>
<td></td>
</tr>
<tr>
<td>Competition</td>
<td>Allelogens; shading; substrate occlusion</td>
<td>Allelogens; shading; substrate occlusion</td>
<td>Shading; substrate occlusion</td>
<td>Allelogens; phagotrophy</td>
<td>ND</td>
<td>ND</td>
<td>Allelogens; phagotrophy</td>
<td>Allelogens; phagotrophy(?)</td>
</tr>
<tr>
<td>Reproduction/propagation/dispersal</td>
<td>Asexual reproduction; akinetes, dormant cells/colonies, hormogonia</td>
<td>Asexual reproduction zygosporae; dormant cells, palmelloid forms</td>
<td>Asexual reproduction auxospores; zygosporae; resting cells</td>
<td>Asexual reproduction auxospores; cysts, palmelloid forms</td>
<td>Cysts</td>
<td>Cysts</td>
<td>Asexual reproduction cysts</td>
<td></td>
</tr>
</tbody>
</table>

*Adaptations to minimize losses via cell damage (photochemical; environmental extremes (pH, temperature, salinity, desiccation), sinking, advective losses, predation/pathogens)*

| Photooxidation | Antenna pigments, phycobilisomes; carotenoids/other protective pigments/sunscreens, buoyancy; ROS scavengers | Antenna pigments (low light); carotenoids; motility | Antenna pigments, motility/benthic | Antenna pigments, motility | Diurnal colour change; motility | Antenna pigments, motility | Antenna pigments, motility | Antenna pigments, motility |
| Temperature | High/low temperature optima; akinetes sheath/mucilage/capsules | ND | Low temperature (high PUFA content) | Low temperature (high PUFA content) | ND | ND | Low temperature (high PUFA content) | ND |
| pH | Akinetes/sheath/mucilage/capsules | Mucilage | Mucilage | ND | Low pH | ND | ND |
| Salinity | Akinetes/sheath/mucilage/capsules | Cell wall; osmoprotectants | ND | ND | ND | ND | Salinity-tolerant (*Prymnesium*) | ND |
| Desiccation | Akinetes/sheath/mucilage/capsules | Mucilage | Mucilage (P) | Mucilage | ND | Cysts | Cysts | Cysts |
| Sinking | Gas vesicles; colonial forms; sheath/mucilage | Flagella; colonial forms | Mucilage; flagella; colonial forms | Flagella; colonial forms; mucilage | Flagella | Flagella | Flagella | Flagella |
| Advective losses (currents/scouring) | Mucilage, “holdfasts” | Holdfasts | Stalks (B) | Mucilage, stalks | NA | NA | NA | NA |
| Predation/pathogens | Size (colonial forms), mucilage; cell wall; toxins, allelogens, grazer deterrents | Size (colonial forms), spines; mucilage; cell wall; motility | Size (colonial forms), cell wall; toxins, allelogens, grazer deterrents | Size (colonial forms), motility; toxins, allelogens | Motility; toxins, allelogens | Trichocysts; mucilage; motility; toxins, allelogens | Mucilage; motility; swimming; toxins (dasmotrophy) | Size; cell wall (thecate), spines; toxins, allelogens |
II PLANKTONIC BLOOMS

A Prokaryotes

1 Cyanobacterial Harmful Blooms (cHABs)
(H. Paerl and S. Watson)

The prevalence of cyanobacteria in inland waters attests to their collective capacity to maximize growth, minimize losses, and achieve dominance, often in highly competitive species assemblages. Planktonic cHABs can develop surface accumulations across vast areas that can be visible from space, as seen in recent satellite imagery of mid-to-late-summer blooms of Microcystis, Anabaena, Planktothrix, and Aphanizomenon in Lakes Erie, Winnipeg, and Lake of the Woods (Fig. 1A and D; Binding et al., 2010; Kling et al., 2011; Steffen et al., 2014). Bloom-forming taxa belong to all major morphological groups of cyanobacteria (Chapters 3 and 4) and include planktonic colonial forms (e.g., Microcystis, Woronichinia), picoplankton (e.g., Synechococcus), and N$_2$-fixing and nonfixing filaments in planktonic (e.g., Anabaena, Gloeotrichia, Aphanizomenon, Cylindrospermopsis, Nodularia, Planktothrix, Pseudanabaena) and benthic habitats (e.g., Lyngbya, Oscillatoria, Phormidium, Scytonema) (Oliver et al., 2012; Paerl and Otten, 2013).

i Harmful Effects

Many cyanobacteria produce toxins and/or malodorous compounds (Section IV, Chemical Ecology). Toxic cHABs (i.e., toward humans) have been targeted for remediation in North America and worldwide since the mid-1900s, and although their potential toxicity was only formally recognized in the mid-1900s, these blooms were linked to cattle deaths as early as 1878 (Rose, 1953; Carmichael, 2008). Toxic and nontoxic cyanobacterial blooms degrade drinking water supplies, recreational waters, and shorelines and threaten human and ecological health; they cause fish and shellfish tainting, foul intakes and beaches, affect property value, and cause significant loss of income to tourist and aquaculture industries (Fig. 1).

ii Factors Influencing Growth

Over their evolutionary history (ca. 2 BY), cyanobacteria have developed mechanisms that allow them to survive and exploit a wide range of environmental conditions and facilitate the mass proliferation of many of the nuisance bloom-forming cHAB taxa (Table 1; Chapters 3 and 4). These mechanisms include (1) opportunistic, luxury phosphorus (P) uptake and storage in polyphosphate bodies, (2) N$_2$-fixation by heterocytes or vegetative cell compartmentalization, (3) inorganic carbon concentrating mechanisms (CCMs; located in the carboxysomes), (4) siderophores and other chelators for trace metal (Fe, Mn) scavenging, (5) photo-adaptive and protective pigments, (6) motility (benthic forms) and buoyancy regulation, (7) dormant resting stages (e.g., akinetes), (8) heterotrophic growth, (9) protective sheaths and capsules, and (10) physical/chemical grazing and pathogen defense mechanisms.

a Nutrients

Empirical, multi-lake studies indicate that the risk of cyanobacterial dominance and blooms is most strongly related to total P: oligotrophic waterbodies with low P levels (generally <5 μg L$^{-1}$ total P) typically do not support cHABs (Downing et al., 2001; Schindler, 2012; Beaulieu et al., 2014). N may also become limiting and influence species composition and biomass in a given water body or water layer, often in late summer, and N$_2$-fixing (diazotrophic) cHABs can constitute significant sources of bioavailable N to the ecosystem (Beversdorf et al., 2013; Paerl and Otten, 2013). Other local and regional factors may moderate the vulnerability of a water body to these blooms and its response to nutrient management (Scheffer et al., 1997; Dai et al., 2012; Carey et al., 2012; Huber et al., 2012; Beaulieu et al., 2014). For example, a recent postrestoration “relapse” in the Great Lakes highlights how both the total amount and the nature of nutrient inputs influence the risk of HAB development. In the 1980s, binational restoration efforts focused on controlling point sources (end-of-pipe) of P-enriched wastewater discharge to the Great Lakes to reduce severe blooms of diazotrophic cyanobacteria such as Aphanizomenon. This management strategy was largely successful, and by the early 1990s, there was a significant reduction in both P loading and these blooms (Makarewicz and Bertram, 1991). Yet in the past decade, Lake Erie and more eutrophic inshore areas of the other Great Lakes have seen a marked resurgence of cHABs, which, in contrast to most of the prerestoration blooms, have a greater predominance of nonfixers such as Microcystis aeruginosa and Planktothrix aghardhii/suspensa (Nicholls, 2011; Steffen et al., 2014). Importantly, while there has been little change in the total external nutrient loading to the Great Lakes, these inputs have shifted in timing, distribution, and bioavailability. Predominantly particulate point source inputs have been replaced by more bioavailable nutrient loads (PO$_4^{3-}$, phosphonate-P from herbicides, NO$_3^-$, and urea-N) from diffuse and nearshore sources (e.g., agricultural runoff, urban stormwater; Stumpf et al., 2012). Other
factors have also been linked to the dramatic rise in chABs in these lakes, such as the introduction of invasive dreissenid mussels, which have engineered significant changes in foodweb structure and nutrient cycling (Hecky et al., 2004; Bykova et al., 2006). Currently, the magnitude and toxicity of chABs in Lake Erie and other Great Lakes now present significant risks to drinking water supplies, beaches, fisheries, and other sectors (Carmichael, 2013). This was demonstrated by the record Lake Erie bloom in 2011, covering an estimated 5000 km² (almost one-quarter of the total surface area), and in the 2014 Toledo Water Crisis (Davis et al., 2010; Wines, 2014).

BloomS dominated by N₂-fixing cyanobacteria have been linked to the availability of N relative to P (or N:P ratio), although this relationship is widely debated (Smith et al., 1999; Elser et al., 2007; Downing et al., 2001; Conley et al., 2009; Schindler, 2012). Nevertheless, a growing body of evidence highlights the importance of N in chAB composition and toxicity. Early management paradigms predict that eutrophic (P-enriched) freshwaters with low molar ratios of N:P (<15) are more susceptible to N₂-fixing chAB dominance; conversely, systems with N:P >20 are more likely to be dominated by eukaryotic algae and non-N₂-fixing cyanobacteria (Smith et al., 1999; Havens et al., 2003). More recent studies have linked N:P ratios with an increased risk of toxin (microcystin, MC)-producing chABs (Orihel et al., 2012; Harris et al., 2014).

b Other Physico-Chemical Factors

Other factors may limit or favor chAB development, such as the availability of micronutrients (e.g., Fe, Mn), light, mixing/flushing, and temperature. Many cyanobacteria, most notably diazotrophs, have high trace metal requirements (Raven, 1990; Wilhelm, 1995), and their growth may be limited by the availability of these micronutrients (Molot et al., 2010). Under hypereutrophic conditions where excessive nutrient supplies exceed biological needs, blooms can become light-limited, because “self-shading” by high cell densities significantly reduce water transparency.

Hydrodynamics and mixing patterns also influence both the risk and composition of chABs. Bloom development can be restrained by short water residence times, where flushing rates exceed growth rates. In stratified systems, spatial segregation (vertical and horizontal) and buoyancy control can support co-occurring HAB species (both eukaryotic and prokaryotic) in different water layers or zones of the lake. Low-light adapted cyanobacteria such as picocyanobacteria (Synechococcus, Cyanobium), Planktothrix aghardhii, Pl. rubescens, Pseudanabaena spp., and Limnophis (Lynbya) birgei can form metalimnetic blooms that may represent a potent “hidden” source of toxins or odor (Walsby and Schanz, 2002; Camacho, 2006; Serizawaa et al., 2010). Chromatically adapted strains of Planktothrix aghardhii/suspensa also cause toxic blooms under turbid eutrophic conditions (Tonk et al., 2005), and the success of these and other chAB taxa may involve microevolution of locally adapted strains (Bonilla et al., 2012; D’Alelio et al., 2013). This enables their exploitation of waterbodies impacted by a combination of eutrophication and climate change, as seen with the toxin-producing Cylindrospermopsis raciborskii, historically considered a tropical taxa, which has colonized eutrophic lakes in North America and worldwide (Briand et al., 2004; Mehnert et al., 2010; Bonilla et al., 2012).

Similarly, temporal segregation can support a diversity of cyanobacteria and eukaryotes with different environmental optima in the same water body, often resulting in a seasonal succession of bloom species. Nitrogen dynamics, for example, can alter the balance of these species in productive systems, where supplies of biologically available N (NO₃⁻, NH₄⁺) are drawn down rapidly by late winter or spring blooms of eukaryotic algae (e.g., diatoms, flagellates, green algae). Once these N supplies are depleted, diazotrophs such as Aphanizomenon, Anabaena, and Cylindrospermopsis increase in importance, succeeded by nonfixers like Microcystis and Planktothrix, which can assimilate the combined N compounds produced by N-fixers (Fig. 3; Teubner et al., 1999; Beversdorf et al., 2013).

Climate change provides an additional catalyst for the expansion of chABs; warmer temperatures may favor some chAB species (Weyhenmeyer, 2001; Paerl and Huisman, 2008; Kosten et al., 2012; Deng et al., 2014; Fig. 4). Warm, protected surface waters develop more stable vertical stratification, favoring buoyancy-controlling taxa. This may also select for toxic strains (e.g., Microcystis aeruginosa) and the expression of toxin genes, particularly under certain nutrient N and P regimes (Gobler et al., 2007). Many chAB taxa have photo-protective pigments, enabling them to survive excessive irradiance when aggregated as surface scums and at the same time, shade underlying subsurface algal populations (Paerl et al., 1983; Table 1; Fig. 2). Other cyanobacteria, such as Planktothrix spp., can photoadapt to lower light levels of nutrient-rich deeper layers, or turbid waters of eutrophic windswept systems.

As surface waters have warmed, the periodicity and range of some cyanobacteria have expanded, coincident with earlier spring thaw and later freeze-up dates or complete loss of winter ice-cover (Wiedner et al., 2007; Deng et al., 2014). More frequent extreme precipitation events with episodes of high material influx to receiving waters favor chAB taxa that can exploit and store these nutrient pulses, particularly if these events are followed by a protracted warm period or drought (Jöhnk et al., 2008; Aubriot and Bonilla, 2012; Huber et al., 2012).
FIGURE 3 Phytoplankton successional pattern in relation to changes in concentrations of dissolved inorganic nitrogen (DIN; ammonium and nitrate/nitrite) in the eutrophic St. Johns River, Florida. As DIN is depleted, a diatom-dominated assemblage is replaced by N$_2$-fixing cyanobacteria (mainly *Anabaena* spp. and *Aphanizomenon* sp.), followed by increased dominance by non-N$_2$ fixing cyanobacteria (dominated by *Microcystis* spp.), which benefits from the fixed N. Data provided by J. Hendrickson, St. Johns River Water Management District, Palatka, Florida.

FIGURE 4 Effect of temperature on growth rates of major phytoplankton groups and cHAB species common to temperate freshwater and brackish environments. Data points are 5°C running bin averages of percent maximum growth rates from three to four common species within each class (fitted lines are third order polynomials). (Adapted from Paerl and Otten (2013)).
c Top-Down and Foodweb Factors

While bottom-up and physical controls (e.g., hydrology, light, nutrients) are important environmental triggers and commonly used as management targets, top-down foodweb interactions can play a major role in shaping the size and composition of plankton communities and the risk of cHABs (Francis et al., 2014). Defense and counter-defense mechanisms have co-evolved among different species, and include morphological (often related to ingestibility, size, or mucilage), semiochemical (taste/olfactory cues, toxins) and lifecycle timing and behavioral adaptations. There are intriguing examples that highlight both the importance viruses, fungi, bacterioplankton, micro- and macrograzers in HABs (Gilbert, 1990; Brussaard, 2004; Deng and Hayes, 2008; Wilhelm and Matteson, 2008; Short, 2012; Gerphagnon et al., 2013; Mohamed and Al-Shehri, 2013), and the need for more research to elucidate modes of top-down control. Differential susceptibility of individual species to allelogens or predator-prey interactions can have a major influence on community structure and successional dominance patterns. For example, large colonial cyanobacteria avoid predation by size-selective grazers such as Daphnia, while filamentous cyanobacteria can inhibit growth and interfere with the feeding apparatus of zooplankton and benthic invertebrates (Haney, 1987; Gilbert, 1990; White and Samelle, 2014). In addition, some cyanobacteria survive passage through grazer guts (Burns and Xu, 1990), which may influence bloom composition and toxicity. Selective foraging for more suitable prey by raptorial herbivorous copepods can favor the development of cHAB taxa such as Cylindrospermopsis raciborskii (Hong et al., 2013). Exposure to cHABs stimulated by global eutrophication and climate change may further select for toxic HAB strains and/or resistant grazers better adapted to exploit these blooms (Lemaire et al., 2012; Schwarzenberger et al., 2012; Ger et al., 2014). Ecosystem-scale shifts may be engineered by AIS introduced directly (via ballast water, recreational boats and gear, inter-basin water transfer) or through the modification of aquatic environments, creating a niche for opportunistic species and drastically altering material recycling and other in-lake processes (Mehnert et al., 2010; Karatayev et al., 2014; see also Carpenter et al., 2001). For example, the widespread colonization of the Great Lakes by quagga and zebra (dreissenid) mussels in the 1990s enhanced light penetration and nutrient recycling in inshore regions, providing seeding beds for cHABs and a shift toward a dominance of potentially toxic Microcystis species (Bykova et al., 2006).

iii cHAB Management

Control strategies for cHABs can be approached at two levels: a short-term response, aimed at reducing the risk of exposure and associated health effects to humans, pets, livestock, fish, and other organisms, and a longer-term strategy to achieve a more sustained reduction of bloom severity and frequency. Jurisdictional differences in water quality guidelines and standards, bloom risk levels and resources often result in different management strategies within and among countries (Chorus and Bartram, 1999; Chorus, 2013). Methods designed to control cHABs include (1) watershed and in-lake nutrient management, (2) algicides and inhibitors, (3) artificial mixing or aeration, and (4) biological manipulation (Petersen, 1982; Nienhuis and Gulati, 2002; Davis and Scarlett, 2005; MacKay et al., 2014). Most long-term success in has been achieved using the first of these approaches, maintaining constraints to external nutrient inputs, although remediated systems that have been subject to prolonged eutrophication often undergo hysteresis and exhibit delayed recovery and erratic relapses (Cronberg et al., 1999; Scheffer et al., 2001, 2009; Gulati et al., 2008). Dredging can be used to reduce sediment P reserves in smaller lakes, but it is costly, may induce short-term nutrient and contaminant release, and is not practical in large lakes (Petersen, 1982; Cronberg, 1982). Shorter-term bloom control measures can have mixed outcomes. Algicides lyse cells, but can result in a release of cell-bound toxins or odor compounds (Peterson et al., 1995). This approach is not feasible for larger systems or waters used for fishing, drinking water, or cattle watering (Jones and Orr, 1994). Despite their potential toxicity, algicides such as copper sulphate have been widely applied in some countries for cyanobacteria management in drinking water supplies—for example, in the United States and Australia—although this practice has been recently restricted or discontinued in some jurisdictions (HMRC, NRMMC, 2011). Some studies have applied barley straw or its extract to reduce cyanobacterial and other algal blooms in small waterbodies (Xiao et al., 2010). The modest success of this treatment against cHABs appears to be related to the growth-inhibiting phenolics and other compounds released during the degradation of the straw, but it seems ineffective for eukaryotic HAB taxa such as Prymnesium (Grover et al., 2007; Errera et al., 2008). In some cases the cell-bound nutrients that are released by this treatment may actually stimulate cyanobacterial growth (Xiao et al., 2010). Chemical treatment with aluminum sulfate (alum; Steinman et al., 2004; Harris et al., 2014), liming (Prepas et al., 2001), or lanthanum-infused bentonite clay (Robb et al., 2003) is designed to precipitate water column nutrients and form a thin layer on the sediment surface to reduce sediment loading. These treatments require repeated application and a stable sediment surface, and their effectiveness is debated. For example, the success of alum additions depends on lake morphology and dose and may be improved if combined with other strategies (Huser and Pilgrim, 2014; Harris et al., 2014). The toxicological effects of lanthanum-infused bentonite clay are unresolved, and this treatment has mixed results, particularly in waters with high dissolved organic C (DOC)
levels (Meis et al., 2012; Lürling et al., 2014). In smaller water bodies, artificial mixing or aeration may reduce anoxic sediment loading and disrupt buoyancy-controlling cHABs, although this may promote other undesirable cHAB taxa such as *Cylindrospermopsis* (Burford and O'Donohue, 2006). Biomanipulation includes introducing or removing fish, benthic filter feeders, or lytic bacteria and viruses (Kasprzak et al., 2002) to control cHABs and/or reduce sediment nutrient resuspension. Some success has been achieved by manipulating zooplanktivorous, piscivorous, and benthivorous fish (Brett and Goldman, 1997), but such foodweb manipulations can have unexpected or undesirable outcomes (McQueen, 1998; Cronberg et al., 1999). Above all, an established monitoring program is fundamental to the success of any cHAB management strategy, in order to evaluate the response to any of these control measures (Søndergaard et al., 2007; Duarte et al., 2009).

B Eukaryotes: Nonflagellates

1 Diatoms
   (S. Watson)

   i Harmful Effects

   Until the twenty-first century, freshwater diatoms were seldom considered a serious nuisance (Jüttner, 2000; Carotenuto et al., 2005; see also Chemical Ecology, Section IV). In marine systems, blooms of the toxic diatom *Pseudo-nitzschia* are widely reported along the North American coastline as a source of the potent neurotoxin domoic acid, and more recently, of β-N-methylamino-l-alanine (BMAA) (Lewitus et al., 2012; Jiang et al., 2014), but to date no freshwater diatom has been identified as a (human) toxin producer. Similarly, reports of penned fish disease caused by blooms of diatoms with barbed setae have been limited to marine waters (Albright et al., 1993), but given the increasing spread of invasive HAB species (e.g., *Prymnesium*; Section II-C), these marine issues may yet become a threat to inland waters. Nevertheless, planktonic diatom blooms cause other problems in freshwaters, including taste and odor (T&O) and fouling nets and water treatment filters (Cronberg, 1982; Stömer, 1988). These blooms can also impair stream habitat and food webs; for example, some of these taxa show toxic effects toward grazers (Jüttner, 2001; Carotenuto et al., 2005; see also Chemical Ecology, Section IV). The decomposition of planktonic diatom blooms may impair water quality; for example, the degradation of the significant winter blooms of the filamentous diatom *Aulacoseira islandica* in Lake Erie may contribute to the severe annual summer hypoxia (Twiss et al., 2012).

   ii Factors Influencing Growth

   As nonmotile species, turbulence and flow regimes are key factors affecting the seasonal and spatial dynamics of planktonic diatoms. Their blooms in large rivers are exacerbated by reduced flow regimes imposed by dam construction and river regulation, particularly where these is significant anthropogenic nutrient input (Mitrovic et al., 2008; Wang et al., 2012; Yang et al., 2012). For example, maximum densities and blooms of diatoms (e.g., *Aulacoseira italica*, *Stephanodiscus niagarae*, *S. hantzschii*) in the upper Mississippi (Pool 7) were measured near navigation dams, where flow is reduced (Huff, 1986). Severe and frequent blooms of centric diatoms such as *S. hantzschii* in theeutrophic lower Hanjiang River (China) occur during low flow periods, suspending waterworks production and causing severe T&O events in drinking water supplies to 1.25 million people in Wuhan City. Nutrient management in densely populated areas can be challenging, and other management measures such as controlled upstream dam release have been proposed (Yang et al., 2012).

   Diatoms frequently dominate winter blooms in both lentic and lotic systems, demonstrating their ability to persist under low light and temperatures (Kiss and Genkal, 1993; Twiss et al., 2012). Centric diatoms such as *Aulacoseira* spp. can maintain significant benthic populations of resting cells that can persist over extended periods of darkness, very low light, or even anaerobic conditions. These cells can rapidly photoadapt and inoculate surface layers with a significant viable population during periods of high turbulence (Sicko-Goad et al., 1989), and blooms of large planktonic diatoms often occur in shallow lakes, induced by wind action or annual spring and fall mixing events. For example, the periodic inoculation of a well-established deep layer algal maximum of viable *Aulacoseira* frustules effectively doubled phytoplankton biomass in shallow Lake Apopka (Florida) during resuspension events (Carrick et al., 1993). Viable benthic overwintering or resting populations of *Aulacoseira* and other large-celled centric diatoms (*Stephanodiscus niagarae*, *S. binderanus*) may periodically initiate or sustain blooms throughout the growing season (Lashaway and Carrick, 2010; Twiss et al., 2012). On the other hand, during calm conditions rapidly growing, small-celled diatoms may overcome settling losses and develop blooms in the surface layers, as seen in Lake Washington (Huisman et al., 1999; Arhonditsis et al., 2004). Spring diatom
blooms often precede summer cHABs and recently have been occurring earlier in many lakes as a result of climate-related changes in mixing and stratification patterns and ice cover (Winder and Schindler, 2004; Shimoda et al., 2011).

Collectively, field studies suggest that there are differences in nutrient regimes associated with diatom blooms in rivers and lakes. Lotic diatom blooms are commonly associated with high phosphorus levels, while lentic blooms can occur across a range of nutrient regimes, and recent work highlighted the important role of hydrodynamics in these patterns, showing species-specific differences in P uptake strategies under different flow regimes (Wang et al., 2012). This has important implications for management and highlights the need for more research in this area. It is important, however, to note that diatoms are considered beneficial, as a source of high quality lipid-rich food for grazers, with some studies exploring management options that might extend the spring diatom bloom as a means of reducing the length of later cyanobacterial blooms (Goldenberg and Lehman, 2012).

C  Eukaryotes: Flagellates

Marine HABs are often caused by eukaryotic flagellates (Lopez et al., 2008); in fact the term HABs was first popularized in reference to toxic “red tides” of marine dinoflagellates. Flagellate blooms have been reported far less frequently from inland waters and have not been linked to any serious human health issues to date. Nevertheless, it appears that fish kills, rancid/fishy odors, and other inland water quality impairments are now increasingly attributed to these taxa. Encompassing a wide spectrum of nutritional modes, many of these taxa are mixotrophs and do not exhibit the same strong relationship with external nutrient supply as cHABs (Watson et al., 1997, 2008), presenting intriguing challenges for management.

1  Haptophytes

i  Problematic Taxa: *Prymnesium parvum*

(B. Brookes)

a  Harmful Effects

Blooms of the mixotrophic haptophyte *Prymnesium parvum*, also known as “golden algae” and the “Texas tide,” cause extensive fish kills in coastal marine waters worldwide (Moestrup, 1994; Edvardsen and Paasche, 1998), but recently, outbreaks of this species have spread to inland waters. A bloom of *P. parvum* was first recorded in inland waters in 1985, along the Pecos River (Texas; James and De La Cruz, 1989), and since then, blooms of this species have affected at least five river basins in Texas, resulting in severe and widespread fish kills and millions of dollars of economic impacts. The full extent of ecological and economic damage caused by *P. parvum* is not well understood, but this species has now been recorded from inland waters in at least 18 U.S. states and in British Columbia, Canada (Brooks et al., 2011). With the increasing development of reservoirs and other impoundments, coupled with drought-related changes in flushing, evaporation, and salinity, the spread of these blooms in North America and other regions is a major concern.

b  Factors Influencing Growth

Until recently, the major environmental factors promoting the inland invasion of *P. parvum* blooms were largely unidentified, and early inland studies benefited from previous work from coastal and marine systems (Granéli et al., 2012). Research from the past decade suggests that this species’ dynamics in inland waters are governed by a complex set of interacting physical, chemical, and biological factors, which presents significant challenges to the development of an effective management program (Brooks et al., 2011; James et al., 2011; Hayden et al., 2012; Prosser et al., 2012). However, while the relative importance of many of these factors is uncertain, salinity has been identified as a primary environmental trigger for *P. parvum* outbreaks. Data from laboratory experiments and a variety of inland waterbodies indicate that this species does not reach bloom densities at salinity levels <1 ppt (Patino et al., 2014). Above this salinity threshold, the risk of *P. parvum* blooms is modified by other factors, including low flow, pH, temperature, nutrients, algal community composition, grazers, and light. Field data from the Brazos River watershed (Texas) suggest that *P. parvum* has a growth threshold for both salinity and low flow (Roelke et al., 2010, 2011; Schwierzke-Wade et al., 2011).

*P. parvum* is a mixotrophic euryhaline species with a complex lifecycle that allows it to exploit and survive a range of environmental conditions (Fig. 5). Several important mechanisms may provide this species with a selective advantage over other phytoplankton, including allelopathy (Table 1). During its mixotrophic stage, these flagellates can adopt both phototrophic and heterotrophic nutritional modes, and thus exploit alternative sources of energy and nutrients under low ambient supplies. At the same time this strategy can actively reduce the abundance of competing algal taxa (Thingstad et al., 1996). The formation of feeding swarms allows *P. parvum* to attack and consume cells of similar size (including other
algae and even invertebrate predators) that are immobilized by its extracellular toxins (Tillman, 2003; Uronen et al., 2005). A number of different *P. parvum* toxins have been tentatively identified (Igarashi et al., 1998, 1999; Henrikson et al., 2010; Bertin et al., 2012a,b; Chemical Ecology, Section IV). These have far-reaching impacts on aquatic foodwebs, acting against bacteria, ciliates, and fish (Barreiro et al., 2005; Baker et al., 2007, 2009; Brooks et al., 2010).

### Management

Conventional nutrient-based management alone may not be successful in controlling these blooms and other measures; for example, increased flushing rates may be required. The growth rate of *P. parvum* saturates at fairly low ambient nutrient supplies, suggesting that blooms may be promoted even at moderate levels of eutrophication. Under highly eutrophic conditions this species may be outcompeted by other HAB species, such as cyanobacteria (Brooks et al., 2011). Models incorporating hydraulic flow, water temperature, salinity, and nutrient supply, factors known to influence the distribution of inland *P. parvum* blooms, have been used to improve our ability to predict outbreaks of this species in Lake Granbury (Texas; Grover et al., 2012). Molecular methods are also being used to track this (and many other HAB) species (Zamor et al., 2012). Coupled with ongoing research and monitoring, such tools can provide a framework for improved models to strengthen environmental assessment and management.

#### Other Haptophytes

(S. Watson and J. Wehr)

### Harmful Effects

Outbreaks of other harmful haptophytes are not as problematic in inland waters as in marine systems, but in view of the inland spread of *Prymnesium*, we have included *Chrysochromulina* in this discussion. There are also striking similarities in the ecophysiology of these related taxa. Only two of the more than 40 described *Chrysochromulina* species are common to freshwaters, notably *C. parva* and *C. breviturrita*, and these appear to occupy different environmental niches (Chapter 13;
Estep and MacIntyre, 1989). C. breviturrita blooms have been linked to “rotten cabbage” odor events in lakes in New Hampshire and Ontario, while outbreaks both species have been implicated in fish kills (Nicholls et al., 1982; Hansen et al., 1994). However, the alleged ichthyotoxins have not been characterized, and lab assays have not demonstrated toxicity against other organisms (Simonsen and Moestrup, 1997).

### b Factors Influencing Growth

The factors regulating *Chrysochromulina* growth are complex and can involve mixotrophic nutrition. In addition to nutrients, *Chrysochromulina* species have essential organic growth requirements, notably vitamins such as thiamine and cobalamin (B12), which they obtain from microplankton prey via direct ingestion (phagotrophy) or through the release of membrane-weakening allelogens affecting their live prey (dasmotrophy; Nielsen et al., 1990; see also Chemical Ecology, Section IV).

*C. parva* commonly occurs at low to moderate densities as a component of the nanoplankton in a wide range of lakes and reservoirs, but exhibits the capacity to form periodic blooms (Nicholls, 2003). Some evidence suggests this species is most competitive under high PAR and UVR, particularly in remediated meso-eutrophic water bodies with a history of eutrophication (Hylander et al., 2011; Chorus and Schauser, 2011). *C. breviturrita* blooms in more oligotrophic systems with lower pH (5.0–6.0) and high \( \text{NH}_4^+ \) to \( \text{NO}_3^- \) ratios and may have more specific nutritional requirements for trace amounts of selenium (Wehr and Brown, 1985; Wehr et al., 1985). Lab studies indicate that freshwater *Chrysochromulina* species are primarily photoautotrophs, but the wide geographic distribution and intermittent blooms of these taxa also may be related to the ability to access alternative supplies of growth-limiting resources via vertical migration and mixotrophy (Jones et al., 1995). Nevertheless, unlike marine strains, bactivorous behavior has yet to be directly demonstrated by freshwater *Chromulina* species (Parke et al., 1962; Wehr et al., 1985; Callieri et al., 2006).

### 2 Chrysophytes

(S. Watson)

#### i Harmful Effects

Chrysophyte blooms are a frequent source of rancid, fishy, or cucumber-like odors in drinking water supplies in North America, Europe, Asia, and Australia (Jones and Korth, 1995; Yano et al., 1988; Chorus et al., 1990; Watson et al., 1996; Watson and Satchwell, 2003; Zhao et al., 2013; Chemical Ecology, Section IV). These odor events typically occur in oligo-mesotrophic systems as spring, fall, or under ice blooms, fueled by an ability to optimize growth at low nutrient and light levels through vertical migration and/or mixotrophy (Yano et al., 1988; Bird and Kalff, 1989; Watson et al., 2001a,b). Mixed assemblages of bactivorous chrysophytes (e.g., *Chrysophaerella, Dinobryon, Uroglena*) often form population maxima in deepwater layers where bacterial activity is intensified (Siver and Chock, 1986; Bird and Kalff, 1989; Nicholls, 1995). Blooms of the fishy-smelling mixotroph *Uroglena americanana* can undergo strong diurnal vertical migration or form co-existing surface and deep population layers (Yoshida et al., 1983; Nygaard 1996). These blooms have also been implicated in occasional fish kills in Lake Biwa (Japan) (Yano et al., 1988; Kamiya et al., 1979). However, chrysophytes can be an important source of unsaturated fatty acids such as eicosapentaenoic acid (EPA) (20:5ω3) and DHA (22:6ω3), which are essential for planktonic grazers (Brett and Müller-Navarra, 1997; Taipale et al., 2013). Furthermore, laboratory studies with the monad *Ochromonas* sp. (closely related to *Uroglena*) have demonstrated an ability to feed on some cyanobacteria including bloom-forming *Microcystis aeruginosa*, reducing both the biomass and toxin content of this HAB species (Van Donk et al., 2009; Wilken et al., 2014).

#### ii Factors Influencing Growth

Planktonic blooms of golden scaled and unscaled flagellated chrysophytes such as *Uroglena, Dinobryon, Synura, Chrysophaerella*, and *Mallomonas* are common in oligo-mesotrophic north temperate waters (Watson et al., 1996; Domaison et al., 2003; Bock et al., 2014; Chapters 12–14), but also impair more eutrophic systems where they can occur in succession with other HAB taxa (Fig. 6G–J; e.g., Yano et al., 1988; Jütter et al., 1986; Nicholls, 1995; Šimek et al., 1997; Tas et al., 2010). Long-term monitoring and paleolimnological studies suggest that the frequency and intensity of chrysophyte blooms are increasing, likely in response to multiple environmental stressors such as nutrient runoff, climate change, and for some species, acidification (Paterson et al., 2008). Similar to haptophytes, many chrysophytes are mixotrophs and use a bactivorous nutritional strategy to supplement energy and inorganic nutrient supplies, and obtain essential growth factors such as vitamins (Holen and Boraas, 1995).
Chlorophytes and Euglenophytes

Chlorophyte flagellates are not commonly considered as HAB species; however, there are occasional reports of mass developments, with implications for foodweb structure and resilience, and (during bloom decay) anoxia. These taxa often form blooms in small eutrophic water bodies, and while these outbreaks are generally associated with high inorganic nutrient supplies, other factors play a role. Znachor and Jezberova (2005) reported a bloom of the colonial green alga *Pleodorina indica* (Volvocales) in the River Malse (Czech Republic) under conditions of low flow and high temperatures. In Lake Erie, large blooms of *Pandorina morum* in early summer 2003 and 2010 extended into the west basin from the Maumee River, which drains a rich agricultural area, and were first misinterpreted from satellite imagery as cyanobacteria, highlighting one of the potential pitfalls of this technology as a chAB monitoring tool (Millie et al., 2008; Wynne et al., 2012).

*Euglena* is a mixotrophic taxon that commonly blooms in small ponds, wastewater-enriched waters, ditches, and river backwaters. Aquaculture operations are typically enriched with fish and other organic waste, and blooms of *Euglena sanguinea* and *E. granulata* have been linked to significant fish mortality in these systems (Zimba et al., 2004). Recent studies have identified the structure of these apparent ichthyotoxins, which are not currently known to affect human health (see Chemical Ecology, Section IV). Carotenoid-rich species such as *E. granulata*, *E. sanguinea*, and *E. shafiqii* can produce conspicuous green or red scums, some of which show diurnal photoadaptive color change from green at dawn and dusk to bright red at intense midday radiation (Rehman, 1998; Chapter 2; Fig. 2.4D–F). These mixotrophs employ a range of...
nutritional modes from osmotrophy to phagotrophy, enabling them to exploit both inorganic and organic resources under a range of light conditions (Mullner et al., 2001).

4 Dinoflagellates
(S. Watson)

Dinoflagellate blooms are a major concern in marine systems but are generally not considered an issue in freshwater systems, although blooms of large thecate taxa such as *Ceratium* and *Peridinium* species are reported in many lakes (see also Chapter 17). In North America, blooms of *Ceratium* (esp. *C. hirundinella* and *C. furcoides*) have been reported as sources of fishy odors (Palmer, 1962), although this has not been extensively investigated. *Ceratium* blooms have also been implicated in at least one fish kill, although the toxin(s) produced were not known (Nicholls et al., 1980). Subtropical Lake Kinneret experiences annual blooms of *P. gatunense* and *Peridiniopsis* spp., which have generated an important long-term database from field and lab-based mechanistic studies, demonstrating the benefit of combining both approaches to resolve the key factors contributing to HABs (Zohary et al., 2012). Studies also highlight the importance of regime shifts, fungal epidemics, and chemical ecology in dinoflagellate HAB events. There are apparent allelogenic interactions between two bloom-forming taxa, the dinoflagellate *P. gatunense* and the cyanobacterium *Microcystis* sp., which can co-exist in separate water layers (Alster and Zohary, 2007; Roelke et al., 2007b).

5 Rhaphidophytes

i Problematic Taxa: *Gonyostomum semens*
(S. Watson)

a Harmful Effects

*Gonyostomum semens* is a large planktonic flagellate common in many, mostly low-pH ponds and lakes in North America (Chapter 11). Blooms of this species are commonly reported from small shallow and stratified humic lakes in northern Europe and can have severe socioeconomic and ecological effects (Hongve et al., 1988; Lepista et al., 1994; Rengefors et al., 2012; Trigal et al., 2013). Blooms are less common across North America, but have been reported from several small humic-rich (dystrophic) lakes in Ohio (Havens, 1989) and in a boreal lake in northern Ontario (Findlay et al., 2005). Cells contain abundant trichocysts, which discharge long mucilaginous “slime” threads upon contact, causing itching and other skin reactions to bathers. These threads, or an associated (unidentified) toxin, appear to cause cell lysis in at least one co-occurring algal species (*Rhodomonas*; Rengefors et al., 2008). Blooms also create issues with drinking water filter clogging and taste-odor episodes. Outbreaks of this species have been associated with a lowered diversity of pelagic grazers and impaired ecosystem resilience (Lembret et al., 2012; Angeler and Johnson, 2013).

b Factors Influencing Growth

*G. semens* undergoes sexual reproduction in response to changes in water temperature, forming benthic cysts (Figueroa and Rengefors, 2006). Spring recruitment of cysts from sediments back into the water column may contribute to bloom dynamics the following year. The recent increase in *G. semen* blooms documented across many European lakes (e.g., Angeler and Johnson, 2013) has been attributed to the warmer water temperatures (>6°C) facilitating greater cyst germination (Rengefors et al., 2012). However, the factors affecting this species’ successful invasion are not fully resolved, although it is most commonly found in waters with high color and humic levels, moderate-high nutrients, and lower conductivity and pH, which in turn are strongly related to catchment characteristics (Lenard et al., 2014; Pęczula et al., 2015). A comparative study of 11 small eutrophic and hypereutrophic lakes in Poland (average total P > 60 μgL⁻¹) linked a greater abundance of *G. semen* to coniferous forest coverage (>60% of the catchment) and associated dystrophic water chemistry. In comparison, lakes with reduced forest cover were dominated by chlorophytes and cyanobacteria (Lenard et al., 2014). Similar to other HAB species, *G. semen* undergoes diurnal vertical migration and can tolerate prolonged exposure to anoxic conditions; however, this behavior does not appear to be linked to nutrient (phosphate) retrieval and instead may be related to predator avoidance (Pęczula et al., 2013, 2015). Resolving the key factors underlying this species’ success is further confounded by the continuous germination of cysts from the sediment and marked genetic differentiation among populations in different years (Lembret et al., 2012).

III BENTHIC HABS

Over 90% of the world’s lakes are small (<10 ha; <10 m depth) with extensive littoral habitats, and productivity is often dominated by benthic or floating algal mats (Wetzel, 1990). Significant littoral and benthic growth may also occur in bays...
and sheltered coastal areas of larger lakes and rivers, and in some cases these zones may experience severe macroalgal blooms even while offshore regions reflect an oligotrophic or mesotrophic state (Higgins et al., 2008). In streams, productivity is most often dominated by benthic algae, especially with elevated nutrient concentrations (Biggs, 2000; Dodds, 2006; Schneider and Lindstrøm, 2011; Stevenson et al., 2012). However, additional factors, such as riparian shading, flood events, and toxic pollutants, modify the effect of nutrients on these assemblages (Hilton et al., 2006; Duarte et al., 2009; Schneider and Lindstrøm, 2011). Thus in highly turbid or shaded streams, light availability may limit phytobenthos biomass accrual, while high water velocity may increase losses due to sloughing and reduce the capacity to fully utilize ambient nutrient supplies (Freeman, 1986). Top-down controls (and grazer-resistance) can also be a major factor (Heck and Valentine, 2007). In many benthic and littoral zones the key drivers and resultant algal assemblages vary temporally and spatially, depending on local inputs, flow, channel, and bank influences (Hilton et al., 2006; Withers and Jarvie, 2008). Nevertheless, overall patterns in phytobenthos communities can provide insight into underlying mechanisms at ecosystem scales. For example, using combined data from a large number of sites from Norway and Austria, Rott and Schneider (2014) concluded that the ecological optima of benthic algal species were fairly consistent across ecoregions, with total P, pH, and conductivity as the key factors controlling their abundance.

A Prokaryotes

1 Cyanobacteria

(S. Watson)

Recent studies indicate an increase in the range and frequency of benthic cyanobacterial blooms across North America and worldwide. As with planktonic cHABs, benthic blooms are often undetected and challenging to diagnose and control. They are difficult to sample and measure, while ambiguities in species identification and variation in ecological, morphological, and genetic types present obstacles to effective risk management (Quiblier et al., 2012).

i Harmful Effects

Benthic cHABs can represent “hidden” sources of human and foodweb toxins, other allelochemicals and malodorous compounds; degrade habitat; foul beaches, shorelines, and intakes; and inflict substantial ecological and socioeconomic costs (Baker et al., 2001; Izaguirre, 2007; Wood et al., 2012). As with planktonic cHAB species, there is significant inter- and intraspecific variance in the harmful metabolites produced by benthic cyanobacteria, which include hepatotoxins, neurotoxins, dermatoxins, irritants, and odor compounds (Izaguirre, 2007; Wood et al., 2012; see Chemical Ecology, Section IV).

ii Factors Influencing Growth

A diversity of benthic taxa from most major cyanobacterial groups (see Chapter 4) can produce blooms, including species of Lyngbya, Microcoleus, Nostoc, Oscillatoria, Phormidium, Pseudanabaena, Plectonema, and Tolypothrix. These benthic taxa employ many of the ecophysiological mechanisms used by planktonic cHABs to exploit and dominate disturbed areas, although typically they do not possess cellular buoyancy mechanisms such as gas vesicles, and have different environmental optima (e.g., light and substrate; Loza et al., 2013; Table 1). Many benthic cyanobacteria are motile (e.g., exhibit gliding) and have the capacity to supplement key nutrient and energy requirements through heterotrophic growth (Oscillatoria, Lyngbya) or N₂-fixation via heterocytes (Nostoc, Tolypothrix), or within anaerobic areas of benthic mats and sediment interfaces (Microcoleus, Lyngbya) (Philip et al., 1992; Stal et al., 2010). Mats are often heterogeneous in species composition and spatial coverage, and include a consortium of algal, bacteria, and fungal microbes.

iii Problematic Taxa: Lyngbya wollei

Lyngbya wollei is a large diameter (trichomes up to 60 μm), filamentous cyanobacterium with a thick sheath (to 3 μm) and an ability to form dense mats where it occurs. Nuisance blooms of L. wollei have been reported in the United States for over a century, with infestations in Massachusetts and New Jersey dating to the 1800s (Speziale and Dyck, 1992). More recent reports suggest an increase in L. wollei blooms across North America, spanning a wide range of ecological conditions (Joyner et al., 2008; Bridgeman and Penamon, 2010; Foss et al., 2012; Hudon et al., 2014). These events can degrade water quality, cause substantial damage to the recreational and aesthetic value of beaches and shorelines, cause skin irritation, cause T&O in drinking water supplies, and foul industrial water intakes and filter beds. They may also lead to reduced species diversity and impair benthic habitat and food webs.
**L. wollei** is an example of how benthic cHABs may colonize a wide range of habitats and possess diverse ecophysiological and toxicological characteristics. Local populations of **L. wollei** show varying capacities to produce taste-odor, hepatotoxins, neurotoxins, and skin irritants (Foss et al., 2012; Kutovaya and Watson, 2014). This is further confounded by taxonomic ambiguity, and new methods are now being applied to address these blooms. Originally described as **Plectonema wollei**, this species is polymorphic and under some conditions exhibits false branching (a characteristic of the genus **Plectonema**; Chapter 4). Recent phylogenetic analysis showed significant genetic variation among strains from Florida and North Carolina, indicating that **L. wollei** represents a complex of several species (Joyner et al., 2008), which may account for its variance in ecophysiology and habitat preferences. As with many large-celled taxa, **L. wollei** can sequester large cell reserves of P, decoupling growth from external inputs and making it very difficult to identify and moderate nutrient-based controls—particularly when detached bloom material is translocated to shorelines and other areas. This taxon does not possess heterocytes, but is capable of N₂-fixation and heterotrophic growth under locally anaerobic conditions within or under the mat, facilitating its adaptation to a range of inorganic and organic nutrient and energy supplies (Stal et al., 2010).

**B Eukaryotes**

Eukaryotic benthic HABs are not known to produce toxins that directly affect humans, and their categorization as HABs relates to their capacity to impair recreational, commercial, or industrial activities; negatively affect the health or condition of other biota; or interfere with water management (Lopez et al., 2008). The following section highlights some of the more problematic species belonging to two taxa, chlorophytes and diatoms, which have recently emerged as major concerns.

1 **Chlorophytes**

(S. Higgins)

Many of the problems associated with filamentous chlorophytes are derived from their propensity to form large floating or attached mats (Fig. 6A–C). Nuisance chlorophyte blooms are dominated by relatively few taxa, most of which are widely distributed across the North American continent and may be distinguished by one of two growth forms, based on their substratum and mode of attachment. Free-floating and loosely attached forms such as **Spirogyra** or **Hydrodictyon**, when they occur in bloom proportions, are generally limited to static waters and sheltered lake or large river backwaters, particularly during extended periods of calm weather. Attached forms, such as **Cladophora**, are more widely distributed across both lentic and lotic habitats, including high-energy littoral zones, and are primarily associated with hard abiotic surfaces, such as rocks, piers, or docks. However, in some cases, their ability to adhere to the hard surfaces of some biota, particularly mussel shells, can play an important role in their distribution and proliferation. Nuisance proliferations of benthic green algae are commonly quantified in terms of biomass, areal cover, or chlorophyll a, and while there are no clear indicator thresholds that demark HAB densities, several have been proposed (Supplee et al., 2009; Watson and Boyer, 2012; Rott and Schneider, 2014). A “lower nuisance” threshold of 50 g dry mass m⁻² has been used for **Cladophora** in the Laurentian Great lakes (Auer et al., 2010), and 150-200 mg total chlorophyll a m⁻² suggested as a boundary between mesotrophic and eutrophic conditions in rivers (Dodds et al., 1998, 1999; Biggs, 2000).

1 **Harmful Effects**

Benthic chlorophyte blooms can have significant negative ecological impacts that can indirectly affect biota by influencing water velocity, light, nutrients, DO, and pH (Rott and Schneider, 2014). Less attention has been paid to top-down (grazer, pathogen) controls, although there is evidence that invertebrate grazing has the potential to suppress nuisance growth (Sturt et al., 2011). Filamentous and benthic chlorophyte HABs can affect other biota directly or indirectly. Some taxa, such as **Cladophora**, have been referred to as ecosystem engineers, due to their ability to reduce current velocity, increase habitat complexity, act as a substrate for epiphytic algae and bacteria, and produce algal exudates that stimulate epiphyte growth (Ward and Ricciardi, 2010; Zulkifly et al., 2013). While some of these effects are considered beneficial, they are largely transitory under bloom conditions, followed by seasonal sloughing. Algal DOC exudates can play an important role in stimulating the microbial community, increasing O₂ consumption, and altering benthic nutrient cycling (Wyatt et al., 2014).

In addition to ecological effects, aesthetic problems associated with large floating or attached algal mats create negative public perceptions, restrict the use of waterways and beaches for recreational purposes, and reduce property values for adjacent homes (Dodds et al., 2009). In the Laurentian Great Lakes, the decay of massive quantities of **Cladophora** along shorelines is unsightly and noxious smelling and can be confused for raw sewage as a result of the production of indoles and other fecal-smelling compounds during their decay (Brownlee et al., 1984; Higgins et al., 2008). Filamentous algal
blooms also clog fishing nets and water intakes for drinking water, irrigation, and power facilities. A nuclear power facility on the Laurentian Great Lakes reported that fouling of their intake screens by *Cladophora* resulted in numerous shut-downs and cost in excess of $30M over a 12-year period (Hamilton, 2007). *Cladophora* blooms are a major problem for water delivery canals in the western United States, with annual budgets of approximately $3.0M for removing weeds (primarily *Cladophora*) along a 600 km canal providing power to Phoenix and Tempe, Arizona (Lembi, 2003). These and other benthic algal or cyanobacterial mats (and planktonic blooms) create other problems for drinking water supplies; the high levels of DOC released during their decay can react with disinfectants such as chlorine to produce carcinogenic trihalomethanes and other byproducts. High DOC also reduces the life expectancy and adsorption capacity of activated carbon filter beds by competing for binding sites (Kraus et al., 2011; Summers et al., 2013).

Both living and decaying *Cladophora* mats in the Laurentian Great Lakes have been associated with microbes that can be human pathogens, including shiga toxin-producing *Escherichia coli*, *Salmonella*, *Shigella*, and *Campylobacter* (Byappanahalli et al., 2003, 2009; Whitman et al., 2003; Ishii et al., 2006). Presently, most associations between pathogenic bacteria and *Cladophora* mats are correlative and require a source of these microbes such as local tributaries containing human or animal waste products (Zulkifly et al., 2013), but algal mats may enhance their survival and reproduction. *E. coli* and *Enterococci* were found associated with 97% of *Cladophora* filaments washed onto beaches in Lake Michigan, and evidence suggested that survival and growth of these bacteria is enhanced in the algal mats (Whitman et al., 2003; Ishii et al., 2006). Chun et al. (2013) reported that >70% of decaying *Cladophora* mats sampled in the Great Lakes were associated with *Clostridium botulinum*, an anaerobe capable of producing neurotoxins potentially responsible for avian botulism and fish mortality. It is of note here that this issue is not exclusive to chlorophytes; a similar association with fecal coliform has been observed with mats of the cHAB taxa *Lyngbya wollei* along the shoreline of Lake St. Clair (Vijayavel et al., 2013).

### Factors Influencing Growth

Several key factors influence the distribution and abundance of these macroalgae, which also affect other benthic HAB taxa such as cyanobacteria and diatoms.

#### Light Attenuation

Like planktonic blooms, benthic algae can have significant effects on light availability, and surface irradiance can be reduced dramatically within and below floating and attached benthic mats. The irradiance at depth Z (m) in the water column \( I_Z \) can be calculated as \( I_Z = I_0 \times e^{-\eta Z} \), where \( I_0 \) represents surface irradiance (\( \mu \text{M} \text{m}^{-2} \text{s}^{-1} \)), and \( \eta \) is the light extinction coefficient \( (\text{m}^{-1}) \). Higgins et al. (2006) reported \( \eta \) values of 20.30 \( \text{m}^{-1} \) in dense *Cladophora* beds, with more than 90% reduction in \( I_0 \) within about 5 cm of upper mat surface. Even higher coefficients \( (\eta=35-400 \text{m}^{-1}) \), one to three orders of magnitude greater than seen for all but the most turbid waters, have been reported for *Ulothrix* and *Oedogonium* mats (Dodds and Guder, 1992). At the higher end of this range, \( I_0 \) would be attenuated by over 90% at a depth of several millimeters within the mats. Berry and Lembi (2000) estimated that \( I_0 \) was reduced from 1900 to 60 \( \mu \text{M} \text{m}^{-2} \text{s}^{-1} \) (97% decrease) immediately beneath a floating mat of *Spirogyra*. Algal mats can also positively influence light, filtering and retaining particles that otherwise would be suspended in the water column through natural turbulence (Stevenson, 1996; Dodds, 2003).

#### Water Velocity

Water velocity has a significant effect on on algal distribution, composition, and metabolism in lentic and lotic environments (Biggs, 1996; Dodds and Biggs, 2002; Frossard et al., 2014). Conversely, the development of floating and submerged algal mats in turn influences water velocity. At relatively small scales, boundary layers can develop adjacent to algal mats that constrain advective mixing and exchange of gases and solutes with surrounding waters (DeAngelis et al., 1995). In lotic environments, the attenuation of water velocity within dense periphyton mats has been described by \( U = U_{\text{avg}} \times e^{-\nu z} \), where \( U \) and \( U_{\text{avg}} \) represent the water velocities at depth \( z \) (mm) and the previous depth increment \( z-d \) respectively, and \( \nu \) represents the velocity attenuation coefficient (Dodds and Biggs, 2002). Velocity attenuation coefficients of 0.3-0.5 mm\(^{-1}\) were described for dense mats of *Ulothrix*, indicating that 3-4 mm within the mat, surface velocities were attenuated by >90% (Dodds and Biggs, 2002). In combination with light attenuation and the effects on photosynthesis, velocity gradients may be associated with strong gradients in dissolved \( O_2 \) and \( pH \); thus \( O_2 \) may be supersaturated at the mat surface and anoxic within several mm into the mat (Dodds, 2003). At larger spatial scales, filamentous algal blooms also have significant effects on water velocity and retention and nutrient cycling. Dense algal coverage of large areas—for example, by filamentous chlorophytes—can greatly reduce flow rates and water storage capacity of streams, irrigation canals, and drainage ditches, and in some cases lead to flooding, increased evaporative losses and altered nutrient cycles (Joska and Bolton, 1996; Lembi, 2003; Oberholster and Botha, 2011).
c  Dissolved Oxygen and pH

Anoxia and high pH are important problems affecting aquatic biota, and with widespread eutrophication and associated proliferation and decomposition of organic material, this has become a major concern for chlorophyte blooms as well as other HABs (Dodds and Welch, 2000). Low DO and high pH associated with blooms of filamentous chlorophytes have been linked to fish mortality (Smith et al., 1999; Dodds and Welch, 2000; Klemencic et al., 2010). The creation of stagnant zones by dense algal mats can induce strong vertical gradients in DO and pH (Dodds, 2003, 2006). As these mats proliferate, their influence over surrounding waters increases, resulting in the potential for large shifts between supersaturated DO during daylight and anoxic conditions at night. Dineen (1953) reported that DO and pH in a small pond were strongly controlled by filamentous green algae such as Hydrodictyon and Spirogyra, and following Hydrodictyon die-off, daytime DO was depleted from >100% to ~7%. Flory and Hawley (1994) linked Hydrodictyon blooms with diurnal DO fluctuations between 34% and 200% saturation in a coastal freshwater lake, while Morgan et al. (2006) reported that 64% of the variance in diurnal DO within agricultural streams in Illinois was explained by filamentous algal biomass, primarily Cladophora.

d  Nutrients

Filamentous algal mats have both direct and indirect effects on nutrient dynamics. During growth, benthic algal blooms act as a nutrient sink and can deplete N and/or P supplies in surrounding waters. Along the northeast shore of Lake Erie, the spring growth phase of Cladophora produced 12,000 ton of dry mass and removed 15 ton of P within 30 days (Higgins et al., 2005). While macrophyte (angiosperm) stands can release 10% or more of photosynthetically fixed C to the water column as DOC (Carpenter and Lodge, 1986), algal blooms can also be significant DOC sources (Dodds, 2006). Losses of up to 90% of daily fixed C were reported from large stands of Cladophora in Shoe Lake, Michigan, and between 9% and 29% from periphyton mats in an Alaskan fen (Cheney and Hough, 1983), and between 30% and 100% in Lake Michigan, depending on nutrient conditions (Wyatt et al., 2014). In general, rates of DOC release by Cladophora are proportionately greater under nutrient-limited than nutrient-replete conditions (Wyatt et al., 2010, 2014).

iii  Problematic Taxa: Cladophora glomerata

This species occurs across all major in North America biomes except the northern tundra (Dodds and Gudder, 1992; Sheath and Cole, 1992). The wide ecological range and the life history traits of this species likely contribute to its HAB formation in benthic habitats (Whitton, 1970; Dodds and Gudder, 1992; Higgins et al., 2008). The history of Cladophora blooms in the Laurentian Great Lakes provides an effective example of the importance of the interplay of several growth-limiting factors in its ecology and capacity to proliferate. Blooms of this species have been reported from these lakes since the early 1930s (Neil and Owen, 1964), and prior to the earlier-described lake-wide P abatement efforts in the late 1970s, Cladophora biomass ranged from 100 to more than 800 g dry mass m⁻² in shallow areas of Lake Erie. Early efforts to reduce these blooms were successfully engineered via nutrient management; remedial efforts were followed by a dramatic decrease in these benthic blooms through the 1980s and early 1990s (Higgins et al., 2008). However, with the more recent resurgence of Cladophora blooms in these and other water bodies, the link between eutrophication and growth is more ambiguous, making nutrient-based management of this macroalga difficult. It is now evident that several of the key factors controlling the biomass of this species in these lakes, notably light penetration, nutrient recycling, and substrate availability, are strongly influenced by the filtering activity and growth of the invasive dreissenid mussels (Auer et al., 2010; Higgins and Vander Zanden, 2010; Higgins et al., 2012). Other top-down factors may alter conditions, such as predation by invasive gobies on invertebrate grazers, which may relax their grazing pressure on Cladophora (Kip and Ricciardi, 2012).

iv  Other Chlorophytes

Naturally productive water bodies and those with a range of human impacts can experience nuisance growths of other filamentous chlorophytes. These include Pithophora (horsehair algae), and dense attached or free-floating mats of this macroalga have been reported from many environments (John, 2003; Lembi, 2003). During the 1950s, for example, Pithophora blooms were problematic in hundreds of fish ponds in the southeast United States (Lawrence, 1954). Pithophora carries large terminal and intercalary akinetes that survive harsh environmental conditions, making eradication extremely difficult. Some phenotypes of P. oedogonia tolerate low light conditions and high water temperatures (>30 °C), providing an advantage for growth in shallow littoral areas, and biomass as high as 500 g dry mass m⁻² have been reported from a shallow lake in Indiana (Spencer and Lembi, 1981).

As with other HAB taxa, the distribution and abundance of bloom-forming filamentous chlorophytes is regulated by a variety of environmental controls, which in many cases have not been well resolved. Floating mats can be composed of
a mixed assemblage, indicative of overlapping resource optima, as commonly seen with members of the Zygnematales (Mougeotia, Spirogyra, Zygnema) and Oedogoniales (Oedogonium, Bulbochaete; see Chapters 8 and 9). Blooms of these species are not clearly related to nutrient levels; for example, Spirogyra is widely distributed throughout the world and North America in irrigation canals, ponds, littoral areas of large and small lakes, and flowing waters. In temperate climates, Spirogyra blooms tend to develop in spring and early summer, and the floating masses can foul intake pipes and filter beds, as seen in water treatment plants on the St. Lawrence River (Ontario; S. Watson, unpublished). Spirogyra blooms are also reported from aquaculture pens and littoral habitats in Lake Huron, often loosely attached to Cladophora filaments, which can be dislodged during storm events. Filaments grow loosely attached to hard substrata, on submerged aquatic vegetation, or free-floating in quiescent waters and are typically coated with mucilage, slimy to the touch, and rarely colonized by epiphytes. O₂ bubbles from photosynthesis are trapped within the mats, rendering them buoyant, and detached floating masses can cover large areas and shade underlying vegetation in static waters and sheltered bays and backwaters. Oedogonium also proliferates in a diversity of water bodies such as irrigation canals, reservoirs, sheltered littoral areas of lakes, slow moving streams and pond aquaculture operations (e.g., Ferreira et al., 1999; Klemencic et al., 2010). In contrast, blooms of Mougeotia and Zygnema often occur in littoral zones of softwater lakes undergoing early stages of acidification (pH 5.0-6.0; Schindler and Turner, 1982; Turner et al., 1991); several species of these taxa have been recently used as acidification bioindicators (Schneider and Lindstrøm, 2011). Some members of the Characeae (stoneworts; e.g., Chara aspera, C. globularis, Nitellopsis obtusa) can form dense submerged beds in shallow, transparent waters and may impact shoreline areas when washed up on beaches, as described for the southeast shore of Lake Huron (Barton et al., 2013). However, nutrient-caused eutrophication can lead to declines in charophytes in previously clear lakes, apparently due to light attenuation by phytoplankton, as observed in Lake Okeechobee, Florida (Steinman et al., 1997). These macroalgae are often called “stinkweed,” a name likely derived through their production of highly volatile thiols and apocarotenoids (see Chemical Ecology, Section IV).

Some benthic chlorophytes are considered invasive. The stonewort Nitellopsis obtusa is native to Europe and Asia and was first discovered in the St. Clair-Detroit River system in 1983 (Schloesser et al., 1986). This alga has since spread across the Great Lakes and other inland lakes in the northeastern United States, possibly reducing macrophyte and benthic algal diversity in littoral zones (Pullman and Crawford, 2010). Hydrodictyon reticulatum (water net) is widely distributed in North America and globally, in ponds, wetlands, sheltered littoral areas, and slow-moving rivers, where macroscopic nets of large, multinucleate cells (cm to m in size) may limit swimming and fishing and can clog irrigation and drainage canals. While blooms of this species have not been commonly reported in North America, it is regarded as an invasive taxon in the UK, Europe, and New Zealand (Wells et al., 1999; John and Tsarenko, 2002; Lelková and Poulíčková, 2004). Extensive blooms in New Zealand during the 1980s and early 1990s caused significant economic and recreational impacts, with floating mats reaching a coverage of >30 ha (Wells et al., 1999). Another possibly invasive bloom taxon is Ulva (formerly Enteromorpha). It has been reported in North American freshwater bodies for more than 100 years (Collins, 1909; Taft, 1964), but was recently recorded at bloom densities in Muskegon Lake (Michigan) and Lake Michigan (Lougeed and Stevenson, 2004).

2 Diatoms
(B. Whitton)

Although the benthic mats of attached algae that can develop in rivers, ditches, and shallow ponds are usually dominated by cyanobacteria or chlorophytes, they almost always include a community of epiphytic diatoms. When these are abundant enough to color the mats deep brown, detached floating material can superficially resemble sewage and cause public concern. However, in general, benthic diatoms are not widely problematic, with one notable exception. Recently, there has been considerable interest and concern focused on Didymosphenia geminata (“didymo” or “rock snot”), discussed here.

i Problematic Taxa: Didymosphenia geminata

Although this also occurs in lakes, D. geminata has mostly been reported from lotic systems where colonies can increase, coalesce, and form mats of 2 cm or more in thickness and cover much of the channel bottom (Fig. 6D–F). Intense interest began with its discovery in New Zealand in 2004 and the suggestion that it was invasive (Biggs et al., 2006). Since then, there has been much interest and debate about its ecology and invasiveness. Mass growths have been reported in rivers of many countries, including the United States and Canada, leading to numerous publications, government papers, and popular press. Many such reports have been from regions with no previous records of such events. Several major reviews on Didymosphenia ecology and management challenges provide detailed information and a literature resource (Blanco and
Although conspicuous growths of *D. geminata* have been reported in many rivers, they have seldom caused major socio-economic problems. In fact, some of the most productive Atlantic salmon rivers in Norway also have the most extensive *D. geminata* growths (Lindstrøm and Skulberg, 2008). Similarly, in Iceland, there are no clear negative impacts of these blooms on *Salmo salar* populations (Jónsson et al., 2008). However, there have been a few cases of mass growths causing local problems, such as clogged water filters in the River San (Poland), impeding the use of river water for domestic supplies (WIOŚ-Jasoń, 1996). The situation in New Zealand is more problematic, with reported huge growths in some of the South Island rivers and dramatic statements by media and water management agencies about the impact of “didymo” on angling and other tourist activities. One study estimated the cost of these blooms at $158M USD over the eight years post-discovery (Vieglaïs, 2008). Yet there is little published evidence to support this level of concern; in fact, a survey of sites from four New Zealand rivers both with and without *D. geminata* found the highest density of galaxid fish at a site with moderate *D. geminata* growth and few other major differences (Larned et al., 2007). Nevertheless, a similar public response to *Didymosphenia* growths is now occurring in Chile (Sastre et al., 2013; Reid and Torres, 2014).

In North America, the assessment of this concern is mixed. Apart from a single report of eye irritation in swimmers downstream of large mats in a river in Arkansas in 2006, most concern has centered on impacts to sports fishing, such as fouling lines, lures, and flies. A large decline in adult brown trout in Rapid Creek, South Dakota, was linked to the onset of *D. geminata* mass growth in 2002 (Larson and Carreiro, 2008). Conversely, based on salmon productivity records, Bothwell et al. (2008) concluded that *D. geminata* infestation had either no impact or, in some cases, a positive effect on productivity in local rivers on Vancouver Island.

It is important, however, to note these blooms inevitably result in a loss of biodiversity and altered material transfer both within the algal community and across other elements of the foodweb (as do all HABs). For example, a study of two impacted and two nonimpacted sites in Rapid Creek, South Dakota, found a reduced percentage of disturbance-sensitive macroinvertebrate taxa (Ephemeroptera, Plecoptera, Trichoptera), with an increase in Diptera at the two *D. geminata* sites (James et al., 2010). Other authors suggest a shift in the total macroinvertebrate community composition and an increase in its abundance where *D. geminata* occurs (Gillis and Chalifour, 2010; Kilroy et al., 2009). Some insects may exploit *D. geminata* mats as refugia from flow to minimize energy requirements (Gillis and Chalifour, 2010).

As many as eleven species of *Didymosphenia* have been recognized (Whitton et al., 2009; Blanco and Ector, 2013), but thus far, all reports of nuisance growths in rivers are of *D. geminata*. Most records of *Didymosphenia* are from north temperate regions, including a number of fossil sites (Blanco and Ector, 2009; Whitton et al., 2009). While most modern records occur north of 33°, there are reports from South America, Asia, Australia, New Zealand, Europe, and North America (Whitton et al., 2009). Its global distribution is not yet fully known, because the intensity of reports likely reflects differences in sampling effort. However, earlier records from many regions suggest a preference for cool or temperate climates and an apparent absence from tropical locations (Bothwell et al., 2014). Spaulding et al. (2008) provided a distribution map from the United States of the 308 sites where this species is known, which indicated an absence from the southernmost states at that time. Reports of mass accumulations were first noted in streams on Vancouver Island in the late 1980s, which were followed by subsequent reports from New Zealand, Iceland, India, and elsewhere (Bhatt et al., 2008; Whitton et al., 2009; Bothwell et al., 2014). Many of the earliest records of *D. geminata* (from before the last century) are from British Columbia lakes (Lord, 1866; Clemens et al., 1939) and rivers (Northcote et al., 1975; Stein, 1975; Stein and Borden, 1979), showing that the alga is native to this region, but its proliferation as blooms in these rivers is a new phenomenon (Bothwell et al., 2014). Evidence of a temporal shift also exists in Montana streams, where filamentous algae and *D. geminata* covered >10% of substrata on the upper East Boulder River between 1998 and 2003, but by late summer 2004, *D. geminata* formed 100% cover at several sites (Beeson and Mitchum, 2006). *D. geminata* has been recorded recently in 18 rivers in the South Saskatchewan River Basin (Alberta) at more than 80% of the 50 sampling sites, with dense growths at almost half of these sites (A.E. Kirkwood, pers. comm.). In contrast, a sediment core study in Naknek Lake (Alaska) found no statistically significant change in the abundance of *D. geminata* (or an endemic *D. clavaherculis*) between 1218 and 2003 (Pite et al., 2009).

### b Factors Influencing Growth

*D. geminata* occurs primarily on firm rocky substrata, preferably colonizing rough versus smooth surfaces, but also attaches to other surfaces such as submerged plants (Berger et al., 2009a). As with most HAB species, nutrients, light, and water movement have a significant impact on the success of *D. geminata*, modulated by key aspects of this species'
lifecycle and ecophysiology. Most studies indicate that high light intensity has a positive effect on cell density (Whitton et al., 2009; James et al., 2014; Taylor and Bothwell, 2014). James et al. (2014) found that shading by bridges virtually eliminated Didymosphenia geminata growth. Calcium concentration or conductivity are usually quite high at sites with abundant Didymosphenia geminata, at least during the main growing season (Whitton et al., 2009), but current belief on the importance of other environmental factors is based largely on statistical correlations. Kirkwood et al. (2009) observed that mean discharge and pH were significant predictors of Didymosphenia geminata abundance at dam sites in rivers of the South Saskatchewan River basin.

Stalks play a key role in the biodistribution and ecophysiology of this species, particularly in respect to light, nutrients, and flow. Didymosphenia geminata populations overwinter as highly motile cells without stalks. These cells become attached firmly to the substratum in spring and develop stalks, raising the frustule from the surface (Ellwood and Whitton, 2007; Whitton et al., 2009). Cell division at the end of these stalks and resultant dichotomization locates the cells a considerable distance from the point of attachment. Stalk formation poses a high energy and carbon demand on the cell, and thus light intensity and/or day length are likely key factors leading to stalk initiation. The interwoven stalks become densely packed and form large colonies (up to 13 cm in diameter; Bergey et al., 2009b), reducing flow around the mats and the risk of detachment (Larned et al., 2011). Didymosphenia geminata stalk attachment is well adapted to withstand fast-moving water, and physical abrasion is a more important cause of bed disturbance (Cullis et al., 2013).

The matrix of stalks also acts to retain and acquire nutrients. Like many other HABs taxa, Didymosphenia geminata exploits both inorganic and organic sources of P to support growth. In a seasonal study of ambient nutrient fractions and Didymosphenia geminata phosphatase activity, Ellwood and Whitton (2007) identified organic P as the main P source for this diatom, a conclusion supported by the few other studies that have measured both organic and inorganic nutrients (Whitton et al., 2009). During low ambient supplies of inorganic P (i.e., phosphate), Didymosphenia geminata cell division is P-limited (Bothwell and Kilroy, 2011; Kilroy and Bothwell, 2011), and under such conditions, the upper parts of stalks stain strongly for organic P-scapenging phosphomonoesterase activity (Ellwood and Whitton, 2007; Aboal et al., 2012). Stalks effectively extend the cell surface area available for nutrient transport. It is likely that a phosphate gradient in the stalk tube is induced and moderated by the rate of P utilization in the cell, which may also explain the importance of high light intensity and long day length. This is supported by evidence from other studies; Kilroy and Bothwell (2011) showed that when a period of nutrient enrichment was followed by unenriched conditions, Didymosphenia geminata division rates declined by 60% while mean stalk length increased by 250%.

While some researchers attribute the success of Didymosphenia geminata to its invasive nature, others suggest that the changes in its biodistribution simply reflect a response to climatic (warming) and atmospheric (N deposition) changes. There are two opposing interpretations of the collective evidence. Bothwell et al. (2014) proposed that Didymosphenia geminata is an ultra-oligotrophic species, and bloom formation occurs when the SRP concentration is naturally low or reduced to low levels by the process of oligotrophication, but they did not measure organic P in their study. Conversely, Whitton et al. (2009) suggest that the current success of Didymosphenia geminata is largely derived from its capacity to effectively exploit short peaks in organic P during late winter and early spring by hydrolyzing organic P in its stalks. This allows it to competitively exclude other algal taxa, because it can continue to hydrolyze organic P in the water once the stalks are formed and reduce available light and current speed for other benthic algae. There have been few watershed-based studies on its seasonal or spatial distribution. In a survey of 485 streams in the western United States between 2000 and 2003, Weilhofer et al. (2006) found that the presence of tundra within the watershed was the major predictor of Didymosphenia geminata occurrence, while watershed disturbance was the main predictor of its the absence. In a broad study of six rivers across multiple watersheds in Alberta (South Saskatchewan River Basin), Kirkwood et al. (2007, 2009) concluded that sites below dams were significantly more likely to have higher Didymosphenia geminata densities and blooms than were upstream sites.

Overall, the terms “invader” and “invasion” have been applied indiscriminately to any mass growth of Didymosphenia by many researchers and government agencies, even in locations with no previous records of its occurrence or proliferation (Taylor and Bothwell, 2014). Yet as can be seen from the above discussion, the invasive nature of these blooms is not well substantiated by collective evidence. With few historical records and apparently no preserved material, the history of Didymosphenia in New Zealand is unresolved (Whitton et al., 2009). Mats of this diatom were first noted in the Lower Waiau River, South Island, in 2004 (Kilroy, 2008), with subsequent reports from 53 rivers on the South Island by 2007 (Larned et al., 2007). Populations of Didymosphenia have now reached nuisance levels in many New Zealand rivers, where it is classified in as an AIS (Taylor and Bothwell, 2014). A similar AIS designation in other countries, however (Sastre et al., 2013; Reid and Torres, 2014), may not be based on adequate historical records.

Regardless of this debate, if P supplies with a high relative organic content are a key factor driving Didymosphenia geminata blooms, what effects would increased eutrophication have on their distribution and abundance? An example from the Coquet River (Northumberland, UK) may be informative. Didymosphenia was first recorded from this river in the mid-19th century, and mass growths occurred from at least the late 1950s to 2006 (Whitton et al., 2009 and author’s observations). As more
eutrophic species have recently increased in this system (e.g., *Cladophora glomerata*), *D. geminata* blooms have disappeared; the species now occurs only occasionally in benthic assemblages. Similar decreases in blooms of *D. geminata* mass growths have been observed elsewhere (e.g., rivers on Vancouver Island, BC), but their cause has not yet been determined.

**c Management**

Apart from tests in New Zealand on the use of algicides (which likely also kill other algae), the main management approach to *D. geminata* control has been focused on reducing the risk of inoculation to nonimpacted rivers. However, these measures have largely targeted human activities, such as requirements for specific angler boot treads (no felt-soled boots) and cleaning among sites, but have not addressed hydrological or animal vectors, so it is doubtful whether they can effectively control the eventual spread of this diatom.

Attempts to manipulate the competitive success of the diatom have also been attempted. For example, Miller et al. (2009) reported a negative correlation between *D. geminata* abundance and total dissolved P. Slow-release granular fertilizer addition was applied to Rapid Creek (South Dakota) to increase nutrient supply (Larson and Carreiro, 2008). This would also increase the ratio of inorganic to organic P, a measure that may be effective in early spring (Whitton and Ellwood, 2008), particularly if effluent levels of combined N are also minimized to limit cell protein synthesis. However, atmospheric N deposition has already altered N:P ratios in many oligotrophic systems (Taylor and Bothwell, 2014). The overall potential negative effect of such enrichment (i.e., effects on water quality, total periphyton biomass, and species composition) needs to be considered seriously before any treatment is applied and other measures may increase the likelihood of successful *D. geminata* control. For example, flushing large growths from spillways or other structures immediately downstream of dams has been suggested, although an experimental study of scouring in the East River, Colorado, found that post treatment recovery by the diatom was rapid (Lee et al., 2008). The apparent requirement for high light intensity in *D. geminata* growth (James et al., 2014) suggests the possible value of riparian planting to increase shade and reduce growth.

Modeling efforts to predict the future distribution of *D. geminata* have been developed for New Zealand, North America, and Chile. These are empirically derived models based on correlations with selected environmental factors (Kumar et al., 2009; Rost et al., 2011), hence their capacity to provide effective management tools is limited. A more successful modeling framework might be better achieved using a combination of empirical, mechanistic, and ecosystem constructs (Kim et al., 2014). This could lay the groundwork for a more rational, science-based consensus on whether this diatom is truly an invasive species or if increased bloom frequency simply reflects its ability to exploit aquatic habitats that have been altered by human activities.

**IV CHEMICAL ECOLOGY OF HABS (SEMIOCHEMICALS)**

(S. Watson)

Cyanobacteria and eukaryotic algae are rich sources of secondary metabolites, many of which play key roles as intracellular chemical signals. While the importance of these semiochemical interactions has long been acknowledged in marine systems, freshwater researchers have been slow to recognize their significance (Hombeck and Boland, 1998), despite the fact that algal cells actively interact with their environment with a myriad of chemical cues and signals (e.g., Caldwell et al., 2004; Brönmark and Hansson, 2012). Much of the research and management effort has focused on a select number of compounds known for their harmful effects on humans or potential socioeconomic value in various industries (Humpage, 2008). Current research is revealing their diverse ecological roles, as photoprotectants, cryogens, pheromones, kairomones, toxins, metabolic inhibitors, antibiotics, teratogens, carcinogens, and grazer deterrents (e.g., Granéli and Hansen, 2006; Hansson et al., 2007; Rohrlack et al., 2008; Watson and Molot, 2013). Individual species or mixed bloom assemblages produce a range of these compounds, which may act synergistically and/or affect different foodweb levels and growth stages (Gilbert, 1990; Zhang et al., 2009). Brönmark and Hansson (2012) provide an extensive review on this topic; here we focus on the two categories of HAB metabolites that have perhaps the most serious socioeconomic effects: (1) volatile organic compounds (VOCs), which are malodorous (but nontoxic to humans at levels found in surface waters), and (2) toxins, which directly affect humans (also nonodorous).

**A Volatile Organic Compounds (VOCs): Taste and Odour**

Algae and cyanobacteria are direct and indirect sources of VOCs that cause T&O in drinking water supplies, recreational waters, and fish and/or shellfish. These compounds are nontoxic to humans (Burgos et al., 2013), but are often used by the public as a primary indicator of the safety and acceptability of water resources. Most people avoid bad-tasting or malodorous water or food, and T&O episodes can lead to restricting the use of public water supplies, waterfronts, and swimming
areas and create substantial costs for water treatment, recreation, fisheries, and aquaculture. Some episodes may render farmed and wild fish and shellfish unpalatable. Poor-tasting tap water is one of the primary causes of the escalating use of bottled water, which is generally less stringently regulated and may contain plasticizers, microbiota, and other contaminants (Foltz, 1999; Gleick, 2010; Hu et al., 2011).

T&O events are caused by the more volatile, but not necessarily most abundant, VOCs present in a sample, all of which contribute to the olfactory “bouquet.” The chemistry of T&O is diverse and includes terpenoids, sulphides, lipid and pigment derivatives, aromatics, hydrocarbons, amines, and other compounds that vary in smell, stability, and response to water treatment (Table 2). The minimum levels at which they can be detected in water, typically measured as their odor threshold concentrations (OTCs), range over several orders of magnitude, with the more potent VOCs detectable at trace (< nanomolar) levels (Young et al., 1996).

### TABLE 2 Examples of Major HAB Semiochemicals, Activity, and Taxa (Bold Type Indicates Major Producer). CYA: Cyanobacteria; CHL: Chlorophyta; DIA: Diatoms (Bacillariophyceae); CHRY: Chrysophyceae; DIN: Dinophyta; CRY: Cryptophyta; HAP: Haptophyceae; ALL: All Decaying Organic Material. Activity Level for (i) VOCs—as Human OTC μg L⁻¹; (ii) Toxins—as LD⁵₀ (μg kg⁻¹ Body Weight: Intraperitoneal Administration to Mouse); Toxins here Indicate Human Toxins Unless Otherwise Indicated; Some of These Compounds, e.g., VOCs, Demonstrate Ecotoxicity

<table>
<thead>
<tr>
<th>Compound</th>
<th>Descriptor</th>
<th>Activity</th>
<th>Tax. Groups</th>
<th>Major HAB Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-Methyl indole</td>
<td>VOC: fecal</td>
<td>CHL</td>
<td>Decaying Cladophora mats, derived from bacterial fermentation</td>
<td></td>
</tr>
<tr>
<td>Skatole</td>
<td>VOC: fecal</td>
<td>CYA; ALL</td>
<td>Cyanobacteria/HAB bacterial fermentation</td>
<td></td>
</tr>
<tr>
<td>4-Methylthio-1,2-dithiolane, 5-methylthio-1,2,3-trithiane</td>
<td>VOC: pungent</td>
<td>CHL: Charales</td>
<td>Chara spp., Nitella translucens</td>
<td></td>
</tr>
<tr>
<td>Dimethyl disulphide; dimethyl sulphide; dimethyltrisulphide</td>
<td>VOC: septic, garlic, putrid; alliaceous</td>
<td>CYA, CHL, DIA, CHRY; AL</td>
<td>Microcystis aeruginosa, Microcystis spp. Anabaena sp., Anacystis nidulans, Plectonema, Oscillatoria spp., Phormidium spp., Nostoc, Oedogonium, Synura, Aulacoseira granulata, decaying material</td>
<td></td>
</tr>
<tr>
<td>Isopropyl disulphide</td>
<td>VOC: alliaceous</td>
<td>0.000006</td>
<td>CYA</td>
<td>Microcystis aeruginosa</td>
</tr>
<tr>
<td>Isopropyl thiol</td>
<td>VOC: pungent; onion, sulfur</td>
<td>CYA</td>
<td>Microcystis aeruginosa</td>
<td></td>
</tr>
<tr>
<td>2-Methylisoborneol</td>
<td>VOC: earthy, musty</td>
<td>0.002-0.02</td>
<td>CYA; other microorganisms e.g., Actinomyces, fungi</td>
<td>Species/strains of e.g., Planktothrix, Synechococcus, Pseudanabaena, Hyella, Jagenina, Tychonema, Nostoc, Phormidium, Oscillatoria, Lyngbya, Porphyrosiphon</td>
</tr>
<tr>
<td>Geosmin</td>
<td>VOC: earthy/musty</td>
<td>0.006-0.01</td>
<td>CYA; other microorganisms e.g., Actinomyces, fungi</td>
<td>Species/strains of e.g., Anabaena, Planktothrix, Cloeotrichia, Symplaca, Aphanizomenon, Leibleinia, Pseudanabaena, Hyella, Calothrix, Tychonema, Nostoc, Geitlerinema, Microcoleus, Phormidium, Oscillatoria, Lyngbya, Schizothrix</td>
</tr>
<tr>
<td>6-Methyl-5-hepten-2-one</td>
<td>VOC: fruity; ester</td>
<td>50</td>
<td>CYA, CHL, DIA, CHRY</td>
<td>Synechococcus, Anabaena cylindrica, Microcystis aeruginosa, Aulacoseira granulata, Synura uvella</td>
</tr>
<tr>
<td>ß-Cyclocitral</td>
<td>VOC: tobacco, flowery; smoky/moldy</td>
<td>19.3</td>
<td>CYA, CHL, HRY</td>
<td>Microcystis spp. (all), Anabaena spp., Dinobryon cylindricum, Synura uvella</td>
</tr>
</tbody>
</table>
### Table 2: Examples of Major HAB Semiochemicals, Activity, and Taxa (Bold Type Indicates Major Producer). CYA: Cyanobacteria; CHL: Chlorophyta; DIA: Diatoms (Bacillariophyceae); CHRY: Chrysophyceae; DIN: Dinophyta; CRY: Cryptophyta; HAP: Haptophyceae; ALL: All Decaying Organic Material. Activity Level for (i) VOCs—as Human OTC μg L⁻¹; (ii) Toxins—as LD₅₀ (μg kg⁻¹ Body Weight: Intraperitoneal Administration to Mouse); Toxins here Indicate Human Toxins Unless Otherwise Indicated; Some of These Compounds, e.g., VOCs, Demonstrate Ecotoxicity—cont’d

<table>
<thead>
<tr>
<th>Compound</th>
<th>Descriptor</th>
<th>Activity</th>
<th>Tax. Groups</th>
<th>Major HAB Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>α-Ionone; β-ionone</td>
<td>VOC: violets</td>
<td>0.007</td>
<td>CYA, CHL, CHRY, CRYP</td>
<td><em>Anabaena</em> spp. <em>Aphanizomenon graciilis, Synura uvella</em></td>
</tr>
<tr>
<td>2,4-Decadienal (trans and cis)</td>
<td>VOC: fishy, rancid</td>
<td>0.07-0.02</td>
<td>CHRY, CRYP, DIN</td>
<td><em>Dinobryon</em> spp., <em>Uroglena americana, S. uvella, Mallomonas papillosa, Cryptomonas rostratiformis, Peridinium willei</em></td>
</tr>
<tr>
<td>2,4,7-Decatrienal (trans and cis)</td>
<td>VOC: fishy, swampy</td>
<td>1.5</td>
<td>DIAT, CHRY</td>
<td><em>Fragilaria</em> sp., <em>Dinobryon</em> spp., *Uroglena americana, Synura uvella, <em>S. petersenii, M. papillosa</em></td>
</tr>
<tr>
<td>2,4-Heptadienal (trans and cis)</td>
<td>VOC: fishy; cod liver oil</td>
<td>5</td>
<td>CYA, CHL, CHRY, CRYP</td>
<td>*Uroglena americana; Anabaena oscillarioides, Fragilaria sp.; Melosira varians, Dinobryon spp., Mallomonas papillosa, Synura petersenii, <em>Hydrurus foetidus, Ulothrix fimbriata</em></td>
</tr>
<tr>
<td>2,6-Nonadienal (trans and cis)</td>
<td>VOC: grassy; cucumber</td>
<td>0.08</td>
<td>CHL, CHRY</td>
<td><em>Synura petersenii</em></td>
</tr>
<tr>
<td>Cis-3-hexen-1-ol</td>
<td>VOC: grass cuttings</td>
<td>70</td>
<td>CHL</td>
<td>Many chlorophytes e.g., <em>Scenedesmus subspicatus</em></td>
</tr>
<tr>
<td>Dictyopterene A; ectocarpene</td>
<td>VOC: seaweed, “ocean”; pheromone</td>
<td>50</td>
<td>DIA</td>
<td><em>Amphora veneta, Cosmophoma parvulum, marine diatoms and pheophytes</em></td>
</tr>
<tr>
<td>1,3,5-Octatriene (fucoserratene)</td>
<td>VOC: geranium</td>
<td></td>
<td>CYA, DIA</td>
<td><em>Asterionella formosa, Anabaena oscillarioides</em></td>
</tr>
<tr>
<td>Skatole</td>
<td>VOC: fecal</td>
<td></td>
<td>CYA, ALL</td>
<td>Cyanobacteria/HAB bacterial fermentation</td>
</tr>
<tr>
<td>Prymnesins</td>
<td>Toxin: ichthyotoxin</td>
<td></td>
<td>HAP</td>
<td><em>Prymnesium parvum</em></td>
</tr>
<tr>
<td>Microcystins</td>
<td>Toxin: carcinogen, hepatotoxin; protein phosphatase inhibition (PPI)</td>
<td>25-150</td>
<td>CYA</td>
<td>Species/strains of <em>Anabaena, Aphanocapsa, Halaplosphon, Microcystis, Nostoc, Oscillatoria, Planktothrix, Anabaenopsis, Arthrospira, Snowella, Woronichinia</em></td>
</tr>
<tr>
<td>Anatoxin-a, homoanatoxin-a</td>
<td>Toxin: respiratory paralysis; death</td>
<td>200-375</td>
<td>CYA</td>
<td>Species/strains of <em>Anabaena, Aphanizomenon, Arthrospira, Cylindrospermopsis, Microcystis, Oscillatoria, Phormidium, Planktothrix, Raphidiopsis</em></td>
</tr>
<tr>
<td>Anatoxin-a(s)</td>
<td>Toxin: respiratory paralysis; death</td>
<td>20</td>
<td>CYA</td>
<td><em>Anabaena</em></td>
</tr>
<tr>
<td>Nodularins</td>
<td>Toxin: carcinogen, hepatotoxin; PPI</td>
<td>30-60</td>
<td>CYA</td>
<td><em>Nodularia spumigena</em></td>
</tr>
<tr>
<td>Saxitoxins (Paralytic Shellfish Poisoning, PSP)</td>
<td>Toxin: respiratory paralysis; death</td>
<td>7.6-10.5</td>
<td>CYA</td>
<td>Species/strains of <em>Anabaena, Aphanizomenon, Cylindrospermopsis, Lyngbya, Planktothrix</em></td>
</tr>
<tr>
<td>Cylindrospermopsin</td>
<td>Toxin: carcinogen; hepatotoxin; PPI; other organs</td>
<td>200-2100</td>
<td>CYA</td>
<td>Species/strains of <em>Aphanizomenon, Cylindrospermopsis, Raphidiopsis, Umezakia</em></td>
</tr>
</tbody>
</table>

(Continued)
As with all HAB issues, T&O management requires an understanding of the biota and factors driving these events. Biological T&O is typically associated with eutrophic systems, but also occurs in oligotrophic, mesotrophic, and restored water bodies (Nicholls et al., 1982; Nicholls, 1995; Watson et al., 2007a). There is a general tendency for managers to focus on plankton, which can overlook the often significant odor potential of benthic producers (Baker et al., 2001; Izaguirre, 2007; Ridal et al., 2007). Importantly, seasonal and spatial dynamics in VOC chemistry and concentration may have significant ecological, socioeconomic, and management implications. VOCs are produced during the growth and decline of different taxa, producing short- and long-term spatial-temporal changes in source-water T&O events. Changes in these patterns can diagnose major drainage basin events (e.g., influencing runoff), seasonal succession in foodweb structure and major ecological regime shifts. Furthermore, VOCs may play an integral part in these changes; evidence now indicates that some of these compounds may act as grazer deterrents, toxins, and pheromones; facilitate adaptation to environmental extremes or are multifunctional; and act at trace levels as feeding deterrents and at higher levels, as toxins (Jüttner, 2001, 2005; Watson, 2003, 2013). This section provides a brief overview, with a focus on some of the most problematic VOCs and their possible functional roles in cell signalling. More extensive reviews are provided by Jüttner (1995), Watson (2003, 2010, 2013), Watson et al. (2001a, 2010).

### 1 Cyanobacterial and Algal Producers

Some VOCs are produced as cell metabolites by a select number of HAB species. Other VOCs are produced in a more general process by these and other cyanobacterial/algal taxa, during the microbial degradation of all algal (and nonalgal) material. This process may both liberate cell-bound algal VOCs and produce other odor compounds, which vary with the chemical conditions (aerobic/anaerobic), microbial community, and nature of the organic material.

Most VOCs are common to several taxonomic groups (Table 2). Together with algal identification, sniffing a water sample (particularly if table salt is added) is a simple and often insightful first step to diagnosing VOCs and their possible source(s). Nevertheless, many T&O events remain untraced, due to their complex nature and a general lack of effective sampling and diagnostic capacity. Other factors that hinder VOC source-tracking include (1) nonalgal sources

<table>
<thead>
<tr>
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<th>Activity</th>
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</tr>
</thead>
<tbody>
<tr>
<td>BMAA</td>
<td>Toxin: putative link to neuro-degenerative disease</td>
<td>CYA</td>
<td>Many taxa, e.g., Anabaena, Cylindrospermopsis, Microcystis, Nostoc, Planktothrix</td>
<td></td>
</tr>
<tr>
<td>Lipopolysaccharide (LPS) endotoxins</td>
<td>Toxin: irritant</td>
<td>CYA</td>
<td>Many taxa, e.g., Lyngbya, Anabaena, Aphanizomenon, Nodularia, Planktothrix, Glocotrichia, Aphanizomenon, Oscillatoria</td>
<td></td>
</tr>
<tr>
<td>Lyngbyatoxins; aplysiatoxin, debromoaplysiatoxin</td>
<td>Toxin: inflamm-atory, dermal toxin</td>
<td>107-250</td>
<td>CYA</td>
<td>Lyngbya wollei</td>
</tr>
<tr>
<td>Euglenophycin</td>
<td>Ichthyotoxin</td>
<td>EUG</td>
<td>Euglena sanguinea</td>
<td></td>
</tr>
<tr>
<td>Anabaenopeptins; micropeptins; oscillapeptin I; cyanobacteria, fischellins, nostocyclamides, etc.</td>
<td>Metabolic enzyme inhibitors, e.g., protease, chitinase</td>
<td>CYA</td>
<td>Many taxa, e.g., Planktothrix rubescens, Anabaena illos-aquae, Microcystis aeruginosa</td>
<td></td>
</tr>
</tbody>
</table>

Where known. Adapted from Watson (2003, 2012); Codd et al., 2005a,b; Wiegand and Pflugmacher, 2005.
(e.g., actinomyces), (2) volatilization or transport away from sites of origin, (3) the lack of a complete catalog of confirmed producers, (4) species misidentification, (5) growth stage and environmental conditions, and (6) loss of production in long-held culture strains.

Cyanobacteria are legendary as sources of malodor, although in fact most taxa produce very little smell during healthy growth. They are mainly known for earthy, muddy, grassy, or sulphurous odors, produced by terpenoids, pigment derivatives, sulphides, and hydrocarbons. Many of these compounds are synthesized during growth and retained intracellularly and/or released into the water during growth or at cell death. Others are only induced at cell lysis though the activation of catalytic enzymes. This mixed mode of VOC production means that cyanobacteria can produce extended or episodic T&O events. A few cyanobacterial species can produce more pleasing odors from terpenoids such as β-ionone (a rose ketone “violet” essence used in many perfumes), although the fermentation derivatives of these terpenoids may be malodorous (Höckelmann and Jüttner, 2005). Chlorophytes, in contrast, are most noted for the production of hay- or grassy-smelling lipid derivatives (oxylipins), such as cis-3-hexenol (leaf alcohol), triggered at cell disruption during death, grazing, or water treatment. Blooms of these taxa are largely odorless during growth. “Golden algae” (diatoms, chrysophytes, and syrno-phytes) are frequent sources of episodic fishy, rancid, or cucumber odors derived from the production of other oxylipins at cell breakdown. Such odors, typical of lipid-rich taxa, have been occasionally described for dinoflagellates, cryptophytes, and some haptophytes but not well characterized for these taxa (Watson, 2003). To date, red algae and euglenophytes are not known as major direct sources of T&O, although Cyanidium caldarium, an unusual rhodophyte from acid hot springs, is a source of floral smelling carotenoid derivatives (Jüttner, 1979).

2. Types of Odors

i. Fishy/Rancid/Oily/Cucumber and Floral Odors: Oxylipins

Taxa with a high cell content of polyunsaturated fatty acids (PUFAs), especially diatoms and flagellates, are common sources of fishy odors, especially during spring phytoplankton blooms and with large growths of epilithic biofilms. Chrysophytes in particular have a high cell lipid content (~30-40% dry weight) and PUFA fraction (~60% total fatty acids; Aaronsen, 1980) and are renowned for these odors, most often caused by polyunsaturated aldehydes (PUAs) such as 2,4-heptadienal, 2,6-decadial, and 2,4,7-decatrienal. Production of these and other oxylipins is triggered only at cell disruption and derived from the oxidative catalysis of ω-3 and ω-6 PUAs such as linolenic, linoleic, and EPAs (Galliard, 1978; Watson et al., 2010). Oxylipins include a variety of compounds and are widely produced by marine and freshwater cyanobacterial and algal taxa. They are highly bioactive, and function as pheromones, grazer deterrents, kairomones, toxins, and tetrarogens (e.g., Watson et al., 2010). For example, they are known to function in marine diatom-grazer interactions, a process that is less well studied in freshwaters (Ianora et al., 2003; Watson and Cruz-Rivera, 2003; Wichard et al., 2005). Their functional role may change with concentration; thus PUAs can act as grazer deterrents at low-moderate levels (as would be encountered in close proximity to a bloom; Jüttner, 2005; Watson et al., 2007b), and toxins or tetrarogens at higher doses (e.g., released from diatom biofilms or ingested material in grazer guts; Jüttner, 2001; Ianora et al., 2003; Watson et al., 2010).

Sporadic episodes of fishy T&O events are often produced during spring and autumn blooms of diatoms (e.g., Asterionella, Fragilaria), chrysophytes (e.g., Dinobryon, Urolema, Chrysophyrella), or synurophytes (e.g., Mallomonas, Synura) (Fig. 6G–J; Watson et al., 2001a). Increased eutrophication can promote higher peak biomass, thus more severe T&O and shifts in oxylipin chemistry to PUAs with more rancid/fetid/oily odors, which may respond differently to treatment (Satchwill et al., 2007). For example, blooms of the colonial chrysophyte Urolema americana cause numerous T&O events in waters with low to moderate and severe eutrophication (Yano et al., 1988; Watson et al., 1996). U. americana produces large amounts of 2,4-heptadienal, which resists treatment by chlorination. The closely related Dinobryon cylindricum produces 2,4-decadial and 2,4,7-decatrienal, which are rapidly oxidized with chlorine. Similar-sized blooms of these taxa in a large drinking water reservoir (Glenmore Reservoir, Alberta) had very different impacts on the treated water supplies (Watson and Satchwill, 2003; Satchwill et al., 2007).

Species from other taxonomic groups (xanthophytes, cryptophytes, dinoflagellates, cyanobacteria, and chlorophytes) may also generate fishy odors (Mallevalle and Suffet, 1987; Rashash et al., 1995; Watson et al., 1999), which in some cases have been attributed to PUAs (Cryptomonas rostriformis, Peridinium sp., Desmodesmus subspecificus; Cotsaris et al., 1995; Watson, 2003). However, these VOCs have not been identified in reported “fishy” events produced by many other taxa (Tribonema, Ceratium, Gymnodinium, Micrystis, Eudorina, Chlamydomonas, Gonium and Volvox); in these cases, such odors may be derived from saturated hydrocarbons, such as heptanal and pentanal, and amines.

Two oxylipins in particular are products of biosynthetic pathways that are not common to most algal taxa and may serve as potential T&O “fingerprints.” The first of these is the heterolytic cleavage product trans, cis-2,6-nonadienal (the
“cucumber PUA”), which is produced in large amounts by two Synura species (S. petersenii, S. uvella). Cucumber odors are a strong indication of the presence of these Synura species in source-waters; trans, cis-2,6-nonadienal has not been associated with other algal taxa to date (although it is found in higher plants; Jüttner, 1995; Wee et al., 1994; Watson and Jüttner, unpublished). Similarly, fucoserratene (trans, cis 1,3,5-octatriene; derived from EPA) is produced as a pheromone by some marine phyophytes (e.g., Fucus), but in inland systems appears to be unique to the planktonic diatom Asterionella formosa, thus providing an identifiable chemical signature of this species, even at low population densities (Jüttner and Müller, 1979). This diatom has a low cell content of other common PUFAs and does not produce the more commonplace PUFAs derived from these precursors (Hombeck and Boland, 1998). Fucoserratene can be induced at all growth stages, but sexual reproduction is rarely observed in A. formosa (Mann, 1999), and this VOC may in fact simply represent a side product of the production of a nonodorous 12-oxododeca-5,8,10-trienoic acid that may act against chytrid parasites commonly afflicting this species (Hombeck and Boland, 1998; de Bruin et al., 2004).

Several factors can influence the VOC chemistry and yield by a given species, which can complicate identifying sources and triggers. Both the chemistry and level of VOCs produced depend on the structure and supply of PUFA substrate, which varies with environmental conditions. For example, mesocosm populations of Uroglena americana (Fig. 6G and H) and Dinobryon cylindricum showed marked differences in VOC yield and chemistry under different light and iron regimes (Watson and Satchwell, 2003). Cell lipid composition also varies with nutritional mode (Gellerman and Schlenk, 1965; Thompson et al., 1992; Brown et al., 1996), although its effect on oxylipin production has not been examined. The mixotrophic chrysophyte Ochromonas danica, for example, increases total cell lipid content and degree of unsaturation when in phagotrophic mode (Schuster et al., 1968), a nutritional strategy used by many other odorous flagellates.

**ii Earthy/Muddy/Musty Odors**

Some of the most frequently reported T&O episodes are caused by two terpenoids, geosmin (trans-1,10-dimethyl-trans-9-decalol) and 2-MIB (2-methylisoborneol). Geosmin and 2-MIB are produced by a diversity of organisms, including bacteria (Actinomyces and Myxobacteria), cyanobacteria, fungi, bryophytes, protozoans, and some plant taxa; they are not, however, synthesized by eukaryotic algae (Zaitlin and Watson, 2006; Jüttner and Watson, 2007). These VOCs are highly potent, with OTCs in the ng L⁻¹ range (Table 2). They are chemically stable and resist natural breakdown, conventional treatment, and boiling (in fact, their odors are even more pronounced in steam from kettles, showers, and saunas). In some cases, geosmin degrades more slowly than the cyanotoxins MCs (Ho et al., 2012). At the range of concentrations typical of most surface waters, geosmin and 2-MIB are nontoxic to humans and most aquatic biota (Burgos et al., 2013; Watson, 2013), but can function in chemosensory predator-prey interactions (Watson et al., 2007b).

Cyanobacteria are the primary sources of geosmin and 2-MIB in inland waters. Hence these VOCs are commonly associated with eutrophic systems where the risk of severe cyanobacterial blooms is high (Jüttner, 1995; Dzialowski et al., 2009; Jüttner and Watson, 2007); however, they can also be problematic in less eutrophic systems (Watson et al., 2007a; Yu et al., 2009). Geosmin is produced by both planktonic and benthic filamentous cyanobacteria, including N₂-fixing and nonfixing forms; 2-MIB is also produced by filamentous cyanobacteria but is not known among N₂-fixers. A very small number of cyanobacteria (e.g., Oscillatoria tenuis) produce both compounds (Wu and Jüttner, 1988). Other microbiota such as fungi and actinomycete bacteria may contribute to geosmin and 2-MIB events during spring runoff or in habitats with significant water-sediment interactions (Klausen et al., 2005; Zaitlin and Watson, 2006; Jüttner and Watson, 2007).

Geosmin and 2-MIB are synthesized throughout cyanobacterial growth and are coupled with cell energetics, photosynthesis, and pigment synthesis. Extra- and intracellular production varies among species, different growth phases, and (in some species) the formation of akinetes and heterocytes and in response to environmental factors such as light, temperature, and nutrients (Wu et al., 1991; Komatsu et al., 2008; Zuo et al., 2009). This can produce variable seasonal and spatial patterns of T&O in source waters, making it difficult to diagnose, anticipate, and therefore proactively control. As with some toxins, cell-bound geosmin and 2-MIB are released with cell damage, during senescence, or with grazing. The dissolved fraction is far more difficult to remove during treatment than the cell-bound (particulate) fraction (Peterson et al., 1995; Peter et al., 2009). New knowledge on the genes and biosynthetic pathways involved in geosmin and 2-MIB production (Giglio et al., 2008, 2010, 2011; Wang and Cane, 2008) has led to the development and application of molecular probes to identify the presence, abundance, and expression of these genes, enabling researchers and water managers to identify the producers, track T&O events, and evaluate the factors influencing their abundance (Auffret et al., 2011; Sua et al., 2013; Tsao et al., 2013; Kutovaya and Watson, 2014). Because some cyanobacteria produce toxins as well as geosmin and 2-MIB (Table 2), these VOCs can signify the presence of potentially harmful taxa in low densities or benthic habitats but they are not a consistent indication of toxicity (Baker et al., 2001; Graham et al., 2010).
iii Sulphurous/Swampy Odors

The emission of Volatile Organic Sulphide Compounds (VOSCs) such as dimethyl sulphide (DMS) is well documented among marine plankton and has a profound influence on global climate and acid precipitation (Bentley and Chasteen, 2004). At a cellular level, these and other biologically produced VOSCs may act as antioxidants, cryogens, and grazer repellents or toxins (Wolfe et al., 1997). VOSCs such as DMS are also major odor constituents of domestic wastewater and the bacterial anaerobic decomposition of blooms and other organic material (Burlingame et al., 2004; Suffet and Rosenfeld, 2007). This process is a common cause of swampy odors in surface waters and a growing issue for drinking water supplies heavily impacted by wastewater and agricultural inputs. However, a select few cyanobacteria and algae actively synthesize VOSCs during cell growth. Charophytes are commonly called “stinkweed,” due to their production of complex thiols (4-methylthio-1,2-dithiolane, 5-methylthio-1,2,3-trithiane), which may act as growth inhibitors against epiphytes and plankton (Anthoni et al., 1980; Berger and Schagerl, 2004). Some strains of the cHAB-forming Microcystis aeruginosa actively produce significant amounts of isopropyl thiols during growth, potentially providing a chemical “signature” of their presence in source waters (Hofbauer and Jüttner, 1988). Together with the carotenoid derivative β-cyclocitril, isopropyl thiols contribute to the distinct sulphurous/tobacco/musty odor of some Microcystis blooms. New evidence shows that these thiols provide protection against the reactive oxygen species often generated under intense photosynthetic activity and surface bloom conditions (Watson and Jüttner, unpublished data). However, these compounds are rarely problematic in drinking water supplies because they are effectively removed by treatment (Tsuchiya et al., 1992). Rotten or sour cabbage odors (similar to DMS) were closely correlated with maximum densities of the haptophyte Chrysochromulina breviturrita in several softwater lakes in Ontario (Nicholls et al., 1982), although attempts to determine a direct link between specific compounds and cells grown in the laboratory have been inconclusive (Wehr et al., 1985).

iv Tobacco-Moldy/Floral Odors

Carotenoid derivatives (apocarotenoids) have a variety of odors, many of which are pleasant (e.g., floral, fruity), and are used widely in fragrance and flavor industries. These VOCs are produced by a diversity of aquatic and terrestrial taxa and are important semiochemicals, acting as kairomones, chromophores, grazer deterrents, growth inhibitors, and toxins. Some of the most commonly detected algal and cyanobacterial apocarotenoids include 6-methylhept-5-en-2-one, nerol, dihydroactinidiolid, α- and β-ionone, and α- and β-cyclocitril (Jüttner, 1981; Henatsch and Jüttner, 1985; Jüttner, 1995; Watson, 2013). Apocarotenoids are derived from carotenes and xanthophylls, pigments that are widely distributed among cyanobacteria and algae. Production is a function of both the type and abundance of these precursor pigments and the carotenoid cleavage dioxygenases inherent to different taxa, and thus can change rapidly with shifts in species and environmental conditions, often independent of algal biomass (Jüttner et al., 1986; Peter et al., 2009). The high degree of substrate specificity of the carotenoid cleavage dioxygenases may prove useful for the diagnosis of select odor compounds and problematic biota. For example, the β-carotene derivative β-cyclocitril is generated in a reaction catalyzed by a carotene oxygenase that is unique to some species of the toxic cyanobacteria Microcystis (Hofbauer and Jüttner, 1988; Takaichi, 2011). This reaction is only induced at cell lysis (Jüttner, 1984a,b; Walsh et al., 1998) and thus β-cyclocitril may provide a diagnostic clue to the composition of a Microcystis bloom and potential for cyanotoxins. As with many other VOCs, β-cyclocitril is also highly bioactive, acting as a powerful grazing deterrent to Daphnia (Jüttner et al., 2010). Similarly, there may be a link between β-ionone and Planktothrix rubescens (Peter et al., 2009), although this apocarotenoid has been reported from water bodies in which this cyanobacterium was not detected (Yu et al., 2009).

B Toxins

1 Cyanotoxins

In inland waters, the most pressing HAB concern from a human health perspective are the toxins produced by cyanobacteria that directly affect humans (Falconer, 2004; Carmichael, 2008; Stewart et al., 2011; Žegura et al., 2011; Merel et al., 2013a,b). These toxins also have pervasive dose-dependent effects throughout the foodweb, which vary even at the same trophic level, depending on susceptibility and mode of exposure (Dvorakova et al., 2002; Ibelings and Havens, 2008; Dao et al., 2010). To date, none of these toxins have been identified from eukaryotic algae, with the possible exception of the neurotoxin BMAA (see below). Cyanobacteria also produce numerous other bioactive compounds (many yet unidentified) that do not affect humans directly but are toxic to other organisms, such as protease and chitinase inhibitors, bleaching agents, and antibiotics (Suikkanen et al., 2004; Rohrlack et al., 2008; Leao et al., 2012). Individual taxa and mixed assemblages typically produce more than one toxin, which can act synergistically or affect growth stages and target species.
Cyanotoxins can be broadly classified into three main groups, hepatotoxins, neurotoxins, and irritants/dermatoxins (Table 2), and are generally named after the first species in which they were characterized. Toxin-producing cHAB species represent the small subset of cyanobacteria with a known potential to produce toxins that directly affect humans, yet relatively few taxa have been fully characterized. It is of note that there is no way of determining by visual or microscopic inspection whether cells have the capacity to produce these toxins.

### i Hepatotoxins

Cyanobacterial hepatotoxins (liver toxins) include three major toxin classes: MCs, nodularins, and cylindrospermopsins (CYLs), which differ in chemical structure and toxicity. Once produced, they are generally stored intracellularly and released when cell integrity is disrupted. Because dissolved toxins are far more challenging to remove than particle-bound material, this has clear implications for algicides and disruptive treatment such as chlorination (Peterson et al., 1995; Ho et al., 2012). Hepatotoxins are generally very stable, and resist degradation and conventional water treatment. Hence, boil-water orders are largely ineffective and may in fact volatilize these compounds in spray or steam (Backer et al., 2008, 2010).

They can be removed from water using strong oxidizing agents or UV, especially in combination with activated charcoal, but in most cases, chlorine is ineffective (Codd et al., 2005a; Westrick, 2008; Westrick et al., 2010). This chemical resiliency increases the risk of public exposure and is a particular concern for MCs, the most commonly reported cyanotoxins across North America and the world. Toxins can persist several weeks after a bloom has disappeared; the rate of degradation by sunlight and bacteria depends on environmental conditions (Chorus and Bartram, 1999; Ho et al., 2012). Water currents can transport toxins from bottom mats into the water column or move toxins, or toxin-containing cells over long distances. Some toxins can be bioaccumulated in bivalves and fish (Zhang et al., 2009; Pawlik-Skowrońska et al., 2013).

MCs are a group of small molecular weight cyclic heptapeptides first identified from *Microcystis aeruginosa*; they are a principal management and research concern. Other cyanobacteria have since been shown to produce MCs and other hepatotoxins, including common bloom-forming taxa such as *Anabaena* and *Planktothrix* (Table 2). Over 90 different MC varieties (congeners) have now been characterized, the most toxic of which is MC-LR, which serves as the basis for drinking water guidelines and standards across the world (e.g., Chorus and Bartram, 1999), although typically, several congeners are produced by individual species or by a multispecies bloom. Exposure usually occurs via ingestion or more rarely, by inhalation (e.g., from showers, saunas, and during recreational activities). Acute dosage level results in massive liver hemorrhaging and heart failure. Human deaths from cyanotoxin poisoning are extremely rare, but illness is not uncommon (Carmichael, 2013). Subacute effects include gastroenteritis, vomiting, fever, flu-like symptoms, ear/eye/throat/mouth irritation, rashes, and blurred vision, but these effects are often unreported or attributed to other common illnesses.

Long-term chronic exposure can lead to kidney and liver damage or increased risk of gastrointestinal cancer (Żegura et al., 2006; Dietrich et al., 2012). Nodularins were first identified from blooms of *Nodularia spumigena* and are particularly problematic in Australia and New Zealand (Chorus and Bartram, 1999), while CYL, a polycyclic uracil derivative, is reported from blooms of *Cylindrospermopsis raciborskii*, *Umezakia natans*, and *Aphanizomenon ovalisporum* and frequently reported in the southern United States, Australia, and Europe (Westrick, 2008; Merel et al., 2013a,b; Rzymski and Poniedziałek, 2014). There is some debate on the phylogenetic and morphological variants of the cyanobacterial producers identified to date, and it is noteworthy that despite the fact that toxic strains of *C. raciborskii* are a major concern in Australia and other regions, to date this species does not seem to be a major CYL producer in North America (Ballot et al., 2011; Yılmaz et al., 2008, 2011; Rzymski and Poniedziałek, 2014).

### ii Neurotoxins

Neurotoxins are a major concern in marine systems, where red tides of dinoflagellates can produce paralytic shellfish toxins (PSTs) that bioaccumulate in filter-feeding shellfish and other commercially important organisms (Hallegraeff et al., 2003). There are fewer studies on the risk and occurrence of cyanobacterial neurotoxins in inland waters (Watson et al., 2008; Merel et al., 2013a,b). These toxins include the alkaloids anatoxin-a, homoanatoxin-a, anatoxin-a(S), and PSTs. They are rapidly degraded once released; thus they are challenging to detect and monitor, and they link to toxicity events. Human and animal exposure to fatal doses leads to rapid death by paralysis of the respiratory muscles. Neurotoxic cyanobacterial blooms have been linked to cattle and wildlife deaths in North America dating back to the late 1800s (Carmichael, 2008; Merel et al., 2013a) and recently to dog mortalities (Puschner et al., 2008). Anatoxin-a has been detected in several
cyanobacterial genera, including *Anabaena* (from which it was first identified), *Oscillatoria*, and *Aphanizomenon*. Heteroanatoxin-a has been identified from *Oscillatoria (Planktothrix)*, and anatoxin-a(S) from *Anabaena*. PSTs have been detected in *Aphanizomenon flos-aquae*, *Anabaena circinalis*, *Lyngbya wollei*, and *Cylindrospermopsis raciborskii* (Table 2). More recently, the nonprotein amino acid BMAA was identified as a neurotoxin and considered to be widely produced among cyanobacteria (Cox et al., 2005). There have been a few reports of this toxin from areas in Florida (Brand et al., 2010), as well as Europe, South America, South Africa, and China (Merel et al., 2013a). However, the importance of BMAA in inland waters remains debated, with other studies unable to detect any significant levels of this toxin, including an extensive number of water samples from North American Great Lakes (Watson and Boyer, 2012). Recent reports of this toxin from marine diatoms and dinoflagellates (Jiang et al., 2014; Lage et al., 2014) indicate that BMAA production may not be limited to cyanobacteria.

iii  Dermatoxic Lipopolysaccharides

Dermatoxic Lipopolysaccharides (LPSs) are common in many systems, as all cyanobacteria contain lipopolysaccharides in their cell walls and LPS concentrations increase with cell density in water. Exposure to sufficient amounts of LPS may cause gastroenteritis, skin and eye irritations, or hay fever. Aerosol contact may cause asthma, eczema, and blistering in nose and mouth membranes.

iv  Standards and Guidelines for Drinking and Recreational Waters

A variety of bloom management and monitoring programs have been developed across the world, some of which include sampling procedures and guidelines/standards for safe levels of cyanobacterial toxins in drinking water and recreational waters. These are largely based on animal ecotoxicity tests and vary considerably in rigor and detail among countries, states, and regions in both the specified toxins (most focus on MC-LR) and maximum advisory levels. Recreational guidelines are inherently problematic to derive and apply; they address waterbodies that can vary dramatically in toxin concentrations within a few hours and/or meters distance due to mixing patterns and prevailing winds, and are often based on total cyanobacterial cell counts, which can include a large number of nontoxic species. Most Canadian provinces have adopted the Health Canada drinking water guidelines for MC-LR in treated drinking water supplies (1.5 $\mu g L^{-1}$). Ontario is the only province to date that has adopted this as a mandated drinking water standard. In the United States, there is no national regulation or guideline for recreational or drinking water for cyanobacterial toxins, but some states (e.g., Ohio) have developed bloom management programs. Recent reviews of human health effects, monitoring and management programs, and drinking/recreational guidelines and standards across different countries including Canada and the United States have been undertaken by the North American International Joint Commission and World Health Organization (Carmichael, 2013; Chorus, 2013).

2  Allelogens

HABs produce a wide array of allelogenic compounds that are not known to be toxic toward humans, but that can have significant effects on other biota. Most of these allelogens are as yet unidentified, except perhaps those that have a clearly identifiable socioeconomic impact. A notable example is the group of ichthyotoxic compounds collectively termed prymnesins, produced by species of *Prymnesium*, including *P. parvum* (described above) and linked with marine fish kills since the late 1800s (Moestrup, 1994). Prymnesins are unstable in the aquatic environment and affected by light, temperature, and pH. They include a mixture of compounds identified as an ichthyotoxin, a cytotoxin, and a hemolysin (Manning and La Claire, 2010, 2013; Schug et al., 2010; Bertin et al., 2014). Recent studies have also identified ichthyotoxic fatty acid amides from *P. parvum*, which increase in toxicity with increasing pH (Bertin et al., 2012b, 2014). It is not yet understood which of these compounds are produced during the life cycle of *P. parvum*, but it remains clear that aquatic toxicity does not directly correlate with cell density, because toxin production per cell varies mainly in response to environmental factors (Skingel et al., 2010; Brooks et al., 2010, 2011). Although ecological impacts of *P. parvum* are most commonly reported as fish kills, some prymnesins also appear to act as allelogens against co-occurring phytoplankton (Fistarel et al., 2003; Granéli and Johansson, 2003; Brooks et al., 2010). *P. parvum* was also demonstrated to impact the reproduction of cladocerans and alter zooplankton community structure (Roelke et al., 2007a).

There are a few reported cases of other ichthyotoxic freshwater taxa, for example, *Chrysocromulina* spp. (Nicholls et al., 1982; Hansen et al., 1994), but these appear to be rare occurrences, and the toxins have not been identified. The few reported ichthyotoxic events caused by chrysophyte flagellates have been attributed to fatty acids, most notably, the unsaturated forms. Fish mortality during a bloom of *Uroglena volvox* in Lake Biwa, for example, was attributed to myristic,
palmitic, and docosatetraenoic acids (Kamiya et al., 1979). Free fatty acids and their hydroperoxides are toxic (Schauenstein et al., 1977; Galliard, 1978), but not freely liberated by intact cells and are rapidly broken down by the catabolic enzymes liberated by dying cells, photooxidation, and microbial activity (Jüttner, 2001; Watson et al., 2010). A number of recent fish kills have also been linked to blooms of Euglena sanguinea (totalling >$1M USD in lost revenue). Several studies have identified the toxin euglenophycin in this and other Euglena species (Zimba et al., 2004, 2010; Gutierrez et al., 2014). Reports of these blooms appear to be increasing, either through an increased occurrence or awareness of their potential toxicity, and were recently recorded from Dillon Lake in Ohio (Ohio EPA, 2013).

Many HABs produce both T&O episodes and toxins, but as noted earlier, T&O cannot be used to reliably predict cyanobacterial toxins. The relationship between cyanobacterial toxins and T&O caused by VOCs such as geosmin, 2-MIB, and β-cyclocitrinal has been examined in several studies as a means of identifying potential sources of risk to human health. However, while the risk of toxins and T&O generally increases with cyanobacterial biomass (Downing et al., 2001; Watson et al., 2008), not all odor-producing blooms are toxic, and not all toxic blooms create odors. Although some authors have reported co-occurrences (Graham et al., 2010), there is no direct physiological link between these metabolites, which are products of different biosynthetic pathways. Toxins are colorless and tasteless, and as with VOCs, vary among and within species in chemistry and yield per cell. Strains of the same species can include producers and nonproducers, while T&O and toxins can also be generated concurrently by different species, in different areas of a water body. In fact, many outbreaks of T&O and toxins are poorly correlated, as shown in studies from North America and China (Watson et al., 2008; Li et al., 2010).

V QUANTIFYING, MONITORING, MODELING, AND MANAGING HABs

(S. Watson, J. Wehr, H. Paerl)

Global reports of inland HABs are increasing rapidly. Widespread eutrophication, basin and shoreline development, expanding urbanization, climate change, and severe storm events are profoundly affecting inland waters. Effects are seen in longer growing seasons, greater runoff, altered mixing patterns, altered nutrient loading, elevated water temperatures, and intensified irradiance. Such changes support more frequent, intense, and widespread outbreaks of HABs and may lead to species more tolerant of extremes in salinity, temperature, pollutants, and UV exposure (Paul, 2008; Paerl and Huisman, 2008).

A number of approaches have been used to manage HABs. Perhaps the most widely used and sustainable of these approaches is based on controlling nutrient inputs, which is often effective in reducing total algal biomass and the growth of nearly all taxa, thereby lessening the risk posed by cyanobacterial toxins. Among the many successful examples of this strategy from North America reduced detergent and sewage-based P inputs, leading to a profound reversal of eutrophication and cHABs in Lake Washington, USA, and the Laurentian Great Lakes (Edmondson and Leland, 1981; Stoermer, 1988). However, recovery can be delayed. Systems with a long history of external P loading have extensive sediment reserves that generate internal nutrient loading and may contain abundant algal propagules. These can continue to fuel HABs for many subsequent years (Petersen, 1982; Cronberg et al., 1999). Other factors confounding restoration efforts include regime shifts (physical, chemical, and biological), demographics, and climate change.

HABs often defy traditional modeling and management frameworks and are difficult to predict and identify. Species outbreaks are regulated at the cell, population, and community levels and occur at different temporal and spatial scales (Smayda, 1997a.b). Cell growth is regulated by endogenous and exogenous processes related to energy and resource supply, particularly irradiance and nutrients. Population growth, ultimately manifested as a “bloom,” represents the net result of past gains and losses from cell division, migration (via buoyancy regulation, motility, sinking, currents, mixing, wind, flushing, etc.), benthic recruitment (seeding), grazing, and parasitism. Bloom and nonbloom assemblages often comprise multiple, concurrent species populations at different growth stages, regulated by different factors. These assemblages typically show extreme spatial and temporal heterogeneity, yet many traditional management models are based on collective measures of entire communities or algal groups, which cannot easily resolve these underlying dynamics. Metrics such as cell numbers, biovolume, chlorophyll and other pigments, fluorescence, δ13C productivity, ATP, DNA, and behavioral and toxicity assays can be used, but it is important to consider (and often overlooked) that each of these quantifies different aspects of abundance or activity. Many of these measures are uncoupled in time and space, some representing instantaneous responses, while others integrate processes over time (Harris, 1980). For example, chlorophyll a (chl-a), one of the most widely used metrics of algal biomass, is a community measure that includes HABs and non-HAB taxa. Chl-a is often inconsistently related to bloom events or algal biomass and varies among taxonomic groups. Fluorescence and photosynthesis can vary on a diurnal or even shorter time scale (Falkowski and Raven, 2007). Remote satellite imagery captures large-scale, surface phenomena but is largely insensitive to species composition and to taxa in deeper strata, although significant progress is being made in this area (Binding et al., 2007, 2010). A more integrated strategy combines a variety of methods
Harmful Algal Blooms (Stengel et al., 2011). Such a polyphasic approach can combine traditional methods (microscopic analyses, paleolimnology, or analytical chemistry) with newly developed techniques such as genomics, which can identify species or strains and measure their co-expression of genes encoding for key cell processes such as C or N$_2$-fixation, P uptake and assimilation, or toxin and T&O production.

Effective HAB management, therefore, requires a multilevel approach that addresses both the immediate and long term-risks posed by HABs and the expectations for improvement (Elser, 1999; Lopez et al., 2008). In many cases, the widely perceived increase in the number and severity of HABs at the local or global scale cannot be rigorously verified, because there are few long-term monitoring programs and the vast majority of water bodies are not monitored. In fact, this increase may, in part, reflect a growing public awareness and reporting, changing demographics, and greater monitoring efforts. Thus, regulatory agencies are increasingly challenged in their attempts to develop and support realistic protection and restoration goals.

Management strategies must also be aligned more closely to the key forcing factors for specific HABs. Modeling provides a useful framework to evaluate and predict both whole ecosystem responses and the risk of HABs under a variety of climate and management scenarios. For example, conceptual and quantitative HAB models can link measures of population, nutrient, and toxin dynamics within the context of legislation such as the U.S. Clean Water Act (Fig. 7; Brooks et al., 2011), or nutrient loading targets under various climate and flow regimes in Lake Erie (Stumpf et al., 2012). Furthermore, a variety of mechanistic and empirical models can be combined to evaluate past and current data and improve our understanding of different aquatic systems, keeping in mind that outliers are important as those data that fit (Kim et al., 2014).

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