9 Brown Tides

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9.1 Background

Brown tides are caused by the pelagophytes *Aureococcus anophagefferens* Hargraves et Sieburth and *Aureoumbra lagunensis* DeYoe et Stockwell. *Aureococcus* has caused destructive ‘brown tide’ blooms in northeast and mid-Atlantic US estuaries for two decades (Nuzzi and Waters 2004), and more recently in South Africa (Probyn et al. 2001). *Aureoumbra* has caused similar blooms in coastal bays in and around the Laguna Madre, Texas, for the past 15 years (Buskey et al. 1997; Villareal et al. 2004). Neither species was known to science prior to the first documented bloom events, but both have since gained notoriety for their ability to disrupt and damage the coastal ecosystems in which they occur.

Although *Aureococcus* and *Aureoumbra* are genetically distinct organisms (DeYoe et al. 1995), they share many similarities. Both contain the unique pigment 19’-butanoyloxyfucoxanthin and are small (4–5 µm for *Aureoumbra* and 2–3 µm for *Aureococcus*), spherical, non-motile cells with simple life cycles (DeYoe et al. 1997). They were originally assigned to the class Chrysophyceae (Sieburth et al. 1988; Buskey and Stockwell 1993), but later examination of their pigments, physiology, 18S rRNA sequences, and morphology led to their formal placement in the class Pelagophyceae (DeYoe et al. 1997). Both contain the pelagophyte-specific sterol, (Z)-24-propylidenecholesterol, which further supports this classification (Giner et al. 2001). While they are sufficiently different genetically to be placed in separate genera, the genetic diversity within each species is poorly described. There has been only one study of intra-species diversity in brown tides, Bailey and Andersen (1999), which examined 14 clones of *Aureococcus* isolated over a 12-year period (1986–1998) from three New York (NY) and New Jersey (NJ) estuaries. Bailey and Andersen found identical sequences for the small subunit rRNA gene, the small subunit RUBISCO gene, and the non-encoding spacer regions of RUBISCO, suggesting little genetic diversity among *Aureococcus* blooms. Despite these genetic similarities, individual *Aureococcus* clones differ in their

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impacts on shellfish (Bricelj et al. 2001) and their susceptibility to viral lysis (Gobler et al. 2004a). However, it is unknown if these differences have a genetic basis.

The first *Aureococcus* blooms occurred simultaneously in the summer of 1985 in several estuaries in the northeastern USA, including Narragansett Bay, Rhode Island, Great South Bay and the Peconic Estuary on Long Island, NY, and putatively in Barnegat Bay, NJ (Cosper et al. 1989; Sieburth et al. 1988; Olsen 1989). Blooms returned to Long Island bays in 1986–88 and have since occurred sporadically in these waters. They have not occurred in the Peconic Estuary since 1995, although low cell densities are still present (up to 10^4 ml^{-1}; Nuzzi and Waters 2004). While *Aureococcus* has been observed in Narragansett Bay in subsequent years, it has not formed a significant bloom there since 1985 (Sieburth et al. 1988). In recent years, blooms have expanded south along the US east coast into bays in New Jersey (Barnegat Bay; Gastrich et al. 2004), Delaware (Little Assawoman Bay; Popels et al. 2003), Maryland, and Virginia (Chincoteague Bay; Trice et al. 2004). *Aureococcus* blooms have also recently occurred in Saldanha Bay, South Africa (Probyn et al. 2001). Low abundances of *Aureococcus* cells have been observed along the entire eastern seaboard of the USA from Maine to Florida, indicating the potential for these blooms to continue to spread north and south of their current range (Anderson et al. 1993; Popels et al. 2003).

The initial *Aureoumbra* bloom in the Laguna Madre and Baffin Bay, Texas began in January 1990 and persisted for nearly 8 years, representing the longest continuous HAB event ever recorded (Buskey et al. 2001). During this time, *Aureoumbra* comprised most of the algal biomass and generally maintained cell densities from $0.5\text{–}5\text{x}10^6$ ml^{-1} (Buskey and Stockwell 1993; Buskey et al. 1997). The bloom terminated in the fall of 1997, but re-emerged during the summer and fall of 1998 (Buskey et al. 2001). Since then it has occurred intermittently in the Laguna Madre system. Low concentrations of *Aureoumbra* cells have also been found in coastal bays across Florida, Texas, and Mexico (Villareal et al. 2004).

During the 1985–1987 *Aureococcus* blooms in eastern and southern Long Island bays, high cell concentrations ($>10^6$ ml^{-1}) substantially increased light attenuation, which caused a large-scale die-off of seagrass beds of *Zostera marina*, a critical habitat for scallops, larval fish, and other species (Dennison 1988). The bloom caused mass mortality and recruitment failure in populations of *Argopecten irradians*, which resulted in the collapse of the multi-million dollar scallop industry in eastern Long Island (Bricelj et al. 1989). The *Aureococcus* blooms also appear to have negatively impacted populations of clams (*Mercenaria mercenaria*) in Great South Bay, which was formerly the largest clam fishery in the state of New York. Subsequent research has established that *Aureococcus* adversely impacts the growth and survival of many algal grazers, including juvenile and adult hard clams (*M. mercenaria*; Bricelj et al. 2001; Greenfield and Lonsdale 2002), larval and adult bay scallops (*A.

irradians; Bricelj et al. 1989; Gallager et al. 1989), adult blue mussels (*Mytilus edulis*; Bricelj et al. 1989), and micro- and mesozooplankton (Lonsdale et al. 1996, Caron et al. 2004). Although a toxin has never been isolated from *Aureococcus*, there is evidence for toxic activity, most likely within the extracellular polysaccharide (EPS) sheath surrounding the cells (Sieburth et al. 1988). This putative toxin deters feeding in bivalves by causing the cessation of cilia movement (Gainey and Shumway 1991). In addition, it has also been argued that *Aureococcus* may be a poor source of nutrition for zooplankton (Lonsdale et al. 1996, Caron et al. 2004).

The ecological impacts of *Aureoumbra* appear to have been similar to those of *Aureococcus*, although the economic impacts have been lower because of a less-developed shellfish industry in and around Laguna Madre. As with *Aureococcus*, the *Aureoumbra* bloom caused a substantial increase in light attenuation, and the resulting shading of the bottom has decreased the abundance of the once extensive sea grass beds (Onuf 1996). There has also been a decrease in the biomass and diversity of benthic invertebrates in the Laguna Madre (Ward et al. 2000). The dominant clam, *Mulinia lateralis*, virtually disappeared after the onset of the brown tide bloom (Montagna et al. 1993), and the dominate polychaete, *Streblospio benedicti*, an important grazer of phytoplankton, has declined in abundance by two orders of magnitude (Buskey et al. 1997). However, population decreases in both species may have begun during the period of high salinity and freezing temperatures prior to the bloom (Buskey et al. 1997). The brown tide bloom also was associated with substantial decreases in the grazing activity, growth, and egg release rates in mesozooplankton (e.g., *Acartia tonsa*), and decreases in the abundance and grazing rates of microzooplankton (Buskey and Stockwell 1993). Like *Aureococcus*, an EPS polymer sheath covers the cell surface of *Aureoumbra*. In feeding experiments with *Aureoumbra*, the presence of high levels of this exopolymer decreased rates of grazing and/or growth in three protozoan species and altered protozoan motility (Liu and Buskey 2000). Liu and Buskey speculated that these effects on grazing and motility may have been caused by the adherence of the exopolymer to cilia on the surface of the protozoans. These cilia are essential for protozoan feeding and motility. Alternatively, the adverse effects may be caused by an unidentified toxin within the polysaccharide sheath, as has been suggested for *Aureococcus*.

9.2 Nutrients and Physical Factors

Although harmful algal blooms in coastal waters have been commonly attributed to nutrient loading, the role of nutrients in the occurrence of brown tides appears to be more complex than a simple nutrient stimulation of brown tide growth. An examination of spatial and temporal patterns of concentrations of

Aureococcus cells and inorganic nutrients indicated that blooms occurred when inorganic nutrient levels were low (Cosper et al. 1989; LaRoche et al. 1997). Moreover, nitrate additions during mesocosm and bottle experiments have consistently yielded reduced *Aureococcus* cell densities relative to those of competing algae (Keller and Rice 1989; Gobler and Sanudo-Wilhelmy 2001a; Gobler et al. 2002, 2004b, 2004 c). The nitrogen-uptake characteristics of *Aureococcus* (low K_s and V_{max} for ammonium) suggest that this species is well adapted to low-nutrient environments. The ability of *Aureococcus* to attain high biomass levels when inorganic nutrient concentrations are low is partly linked to its ability to utilize organic forms of C, N, and P. Cultures (both axenic and non-axenic) and field populations of *Aureococcus* have been shown to obtain nitrogen from a variety of organic compounds, including urea, amino acids, proteins, chitobiose, and acetamide (Berg et al. 2002; Mulholland et al. 2002), and to assimilate organic carbon from glucose and amino acids (Mulholland et al. 2002). Experimental additions of DOM (glucose, amino acids, DOM from marcroalgae) have enhanced the growth and relative abundance of *Aureococcus* during field experiments (Gobler and Sanudo-Wilhelmy 2001a). Dissolved organic nitrogen (DON) and carbon (DOC) are often elevated during bloom initiation (LaRoche et al. 1997; Gobler et al. 2002, 2004b) and reductions in DOC and DON concentrations have been noted with bloom development, a pattern consistent with utilization of these substances by *Aureococcus* (LaRoche et al. 1997; Gobler et al. 2004b). While DON provides an important N source to blooms, heterotrophic C consumption may partly circumvent the need for photosynthetic carbon fixation. This mixotrophy may give *Aureococcus* a competitive advantage over strictly autotrophic algae under severe shading during blooms.

Blooms of *Aureococcus* often occur after ‘pre-blooms’ of other algae, which both draw down inorganic nutrients to low levels and cause gradual increases in more biologically refractory DON and DOC pools (Gobler and Sanudo-Wilhelmy 2001b). Nutrient remineralization processes during, and following these preblooms can result in enhanced DOM levels, which can serve as a source of DON and DOC to subsequent *Aureococcus* blooms (LaRoche et al. 1997, Gobler and Sañudo-Wilhelmy 2001b). Since such blooms usually occur in shallow bays, fluxes from the benthos are important sources of inorganic and organic nutrients (Lomas et al. 2004). Whether sediments serve as a net source or sink for nutrients often depends on the degree to which benthic primary producers (microalgae, sea grass, or macroalgae) utilize nutrients regenerated in sediments (MacIntyre et al. 2004). Brown-tide shading of the bottom causes a net loss of these benthic phototrophs, and this loss provides a source of nutrients and DOM via plant matter decay and recycling processes. This loss also increases net benthic flux of nutrients to the water column due to decreased utilization by benthic phototrophs. Both processes should promote the development of brown tide blooms (MacIntyre et al. 2004).

Considerably less is known about the role of nutrients in the development and persistence of *Aureoumbra* blooms. The initial brown tide bloom in the Laguna Madre and Baffin Bay, Texas developed after an extremely dry period and a rare freeze in December 1989. This freeze caused extensive mortalities of fish and other organisms, and a subsequent large pulse of regenerated ammonium (up to 25 µM; Buskey et al. 1996). The ammonium pulse stimulated the growth of *Aureoumbra* to bloom levels ($\sim 10^6$ cells L^{-1}) in the upper reaches of Baffin Bay during January 1990, but the bloom did not spread to lower Baffin Bay or the adjacent Laguna Madre until June of that year (Buskey et al. 1997). Thereafter, ammonia concentrations plummeted to very low levels (<1 µM) in the Laguna Madre system and remained low during the following year (Buskey et al. 1996). The decrease in ammonia in the Laguna Madre may be attributed to the high demand created by the high *Aureoumbra* biomass. However, there is evidence that this species is also well adapted to low concentrations of available nutrients. Chemostat studies indicate that *Aureoumbra* can grow at extremely low cellular P:C ratios, and thus may be well adapted to low-phosphorus environments (Liu et al. 2001). Moreover, its small cell size, like that of *Aureococcus*, results in a high surface to volume ratio and a thin surface diffusive boundary layer, which should further favor growth of this species at low-nutrient concentrations (Raven and Kubler 2002). *Aureoumbra* utilizes ammonia or urea as nitrogen sources, but is unable to grow on nitrate, usually the most available nitrogen source under high-nutrient conditions (DeYoe and Suttle 1994). In a mesocosm study in the Laguna Madre in the summer of 1999, the addition of 40 µM ammonia to water containing 0.4 µM of that nutrient had no effect on the net growth rate of *Aureoumbra*, suggesting that brown tide growth was not limited by nitrogen availability (Buskey et al. 2003). There have been no studies of the ability of *Aureoumbra* to utilize organic sources of nitrogen, but it is likely that this putative low-nutrient species, like *Aureococcus* and other low-nutrient species, is able to grow on a variety of organic nitrogen substrates. The mixotrophic capabilities in *Aureoumbra* have not been examined.

Physical factors (salinity, temperature, light, and water residence times) can also influence brown tide blooms. Both *Aureococcus* and *Aureoumbra* blooms are associated with high chlorophyll-*a* (chl-*a*) concentrations (30–60 µg L^{-1}) and severe light attenuation. *Aureococcus* is able to maintain a near-maximum growth rate (at 20 °C) at a light intensity of 100 µmol photons m^{-2} s^{-1} (~4 % of noon solar irradiance; Milligan and Cosper 1997; MacIntyre et al. 2004) while *Aureoumbra* is able to do the same at a slightly higher irradiance (150 µmol photons m^{-2} s^{-1}; Buskey et al. 1998). Curiously, the accessory pigments in *Aureococcus* make it best adapted for growth at low levels of blue light, as found in the deep chlorophyll maximum in the open ocean where pelagophytes are commonly found, and less-well-adapted for growth at low intensities of the longer wavelength visible light that occur during brown tide blooms (Yentsch et al. 1989). Based on these observations, Yentsch et al. suggested that *Aureococcus* might be an expatriate open-ocean species. The ability of the two brown-tide species to grow maximally at low light intensities likely contributes to their ability to compete well with non-HAB species during blooms (Milligan and Cosper 1997; MacIntyre et al. 2004).

Aureococcus grows optimally at salinities > 24 PSU and blooms of this species tend to occur during dry years with elevated salinities (Cosper et al. 1989; LaRoche et al. 1997). However, this phenomenon is more likely related to the reduced inorganic nutrient loading from reduced groundwater inputs, rather than salinity per se since the salinities of most bays that experience brown tide blooms rarely fall below 24 PSU (Cosper et al. 1989; LaRoche et al. 1997; Gobler and Sañudo-Wilhelmy 2001b).

Aureoumbra can grow over a wide range of salinities (10–90 PSU) and maintains near optimal growth at salinities of 20–70 PSU at 25 °C (Buskey et al. 1998). This ability to acclimate to a wide salinity range and to grow well at very high salinities appears to have contributed to the initiation of the brown tide bloom in Laguna Madre (Buskey et al. 1998). The Laguna Madre estuary is a shallow (1.2 m average depth) hypersaline lagoon within a semi-arid region of south Texas. Salinities can vary considerably, depending on rainfall, and the initial *Aureoumbra* bloom occurred after a prolonged dry period. It was initiated in the hypersaline upper reaches of Baffin Bay in January 1990, where maximum salinities reached 70 PSU. This salinity was within the range for near-optimal growth of *Aureoumbra*, but well above the optimal range for most algal grazers and competing algal species (Buskey et al. 1998). During the period just before the bloom there was a significant negative correlation between microzooplankton abundance and salinity, with very low abundances ($<10\ \mathrm{ml}^{-1}$) at the highest salinities. The low grazing pressure on *Aureoumbra* associated with the high salinities was likely a contributing factor in bloom initiation (Buskey et al. 1998).

The wide salinity tolerance of *Aureoumbra* also likely contributed to the unprecedented persistence of the bloom. The bloom temporally terminated in the fall of 1997, after intense rains decreased average salinities in Baffin Bay from ~50 to 15 PSU, below the range for optimal *Aureoumbra* growth (Buskey et al. 2001). Thus, the demise of the bloom may have been partly caused by a decrease in brown tide growth and a concomitant increase in the growth rate of competing phytoplankton associated with the lower salinities. In addition, an influx of nutrients accompanying the large freshwater input stimulated the growth of other algae such as the diatom *Rhizosolenia* sp. (Buskey et al. 1998).

Aureococcus blooms under a wide range of temperatures (0–25 °C) and shows optimal growth at ~20 °C (Cosper et al. 1989; Gobler et al. 2002). Blooms typically initiate during late May to early June as temperatures approach 15–20 °C, and decline when temperatures exceed 25 °C (Nuzzi and Waters 2004). However, *Aureococcus* blooms have been observed to persist and even initiate during the fall when temperatures decline, and can persist during winter when temperatures reach freezing levels (Nuzzi and Waters 2004; Gobler et al. 2002).

Temperature may also influence *Aureoumbra* bloom dynamics. Temperatures in the Laguna Madre usually range from 10–15 °C in the winter to ~30 °C in summer, within a favorable range for *Aureoumbra* (Buskey et al. 1996, 1998). In culture studies, the specific growth rate of *Aureoumbra* increased with temperature within the seasonal range, with a rate of 0.25 d^{-1} at 15 °C, 0.62 d^{-1} at 25 °C, and 0.8 d^{-1} at 30 °C (Buskey et al. 1998; Sunda and Hardison, unpubl. data). Thus unlike *Aureococcus*, the highest summer temperatures in the Laguna Madre system appear to favor rapid growth of *Aureoumbra*. The ability to grow over a wide range of temperatures likely contributed to the persistence of the Texas brown tide bloom.

While bays that host frequent *Aureococcus* blooms are known to have high salinities and are relatively shallow, an additional attribute of these bays is their long residence times (up to 100 days), which are associated with low freshwater inputs and low rates of mixing with coastal seawater (Wilson 1995). Similarly, estimates of residence times for the upper Laguna Madre and Baffin Bay, Texas, which host *Aureoumbra* blooms, can range from 300 days to several years (Buskey et al. 1998, 2001). While long residence times clearly permit the accumulation of high algal biomass, they would not necessarily give a competitive advantage to one algal species over another. However, the high biomass and low inputs of external nutrients in these systems create large algal nutrient demand:supply ratios, and hence low concentrations of available inorganic nutrients. Moreover, intense nutrient recycling within these shallow, long-residence time systems promotes the accumulation of DOM (Lomas et al. 2004). Therefore, although the long residence times of these shallow estuaries do not themselves directly stimulate brown tide blooms, the resulting low concentrations of available nutrients and low ratios of inorganic to organic pools of N and P likely favor the net growth of brown tide species.

9.3 Sources of Cell Mortality

Because of their small size, *Aureococcus* and *Aureoumbra* should be efficiently grazed by microzooplankton, whose rapid growth rates should prevent blooms from developing (Sherr and Sherr 2002). However, grazing rates on these species are typically low due to unpalatability, physical interference with grazing, or toxicity. These low rates of grazing mortality have been proposed to be important factors in the initiation and persistence of brown tide blooms (Buskey et al. 1997; Gobler et al. 2002). While the zooplankton are able to actively graze during *Aureococcus* blooms, specific grazing rates on *Aureococcus* can be considerably less (e.g., 30 %; Gobler et al. 2002) than those for competing algae, and lower than concurrent specific growth rates for *Aureococcus*

(Gobler et al. 2002, 2004 c; Caron et al. 2004). Reduced grazing may be partly facilitated by the EPS layer of *Aureococcus*. Another mechanism that may decrease grazing on *Aureococcus* is a microbial trophic cascade in which enhanced grazing by larger zooplankton reduces microzooplankton populations, which in turn reduces grazing on brown tide cells (Sieracki et al. 2004). It appears that this mechanism does not promote Texas brown tides (Buskey et al. 2003).

Aureococcus blooms have waned in their intensity and frequency in some US estuaries (e.g., Great South Bay, NY) and have vanished from others (Peconic Estuary, NY). These systems do not appear to have experienced changes in their chemical or physical characteristics relative to periods when intense blooms first occurred (Nuzzi and Waters 2004). Zooplankton communities can evolve resistance to harmful algae over time via natural selection processes (Hairston et al. 2002). The selective adverse impact of blooms on more sensitive grazer species and more sensitive phenotypes within populations (Caron et al. 2004) should eventually lead to the establishment of grazer communities that are better adapted to co-exist with and consume *Aureococcus*. Recent studies have shown that some NY estuaries, which formerly hosted zooplankton communities that consumed *Aureococcus* at low rates during massive blooms, now have communities that actively graze *Aureococcus* at similar rates to those for other species when brown tide densities are low (10^4 cells ml^{-1}; Deonarine 2005). As such, the recent abatement of brown tides in some Long Island bays (e.g., Peconic Estuary and West Neck Bay; Nuzzi and Waters 2004) may reflect a shift in grazing communities toward an increased ability to feed and grow on *Aureococcus*.

The occurrence of brown tides in Long Island bays may be partly related to the dramatic decline in shellfish populations from over-harvesting in recent decades, and the subsequent loss of this important source of algal grazing mortality. Such a loss of these benthic filter feeders may have shifted planktonic grazing pressure toward zooplankton, which may be more efficient than bivalves at food selection and rejection, including avoidance of *Aureococcus* (Gobler et al. 2002). In support of this hypothesis, mesocosms containing high but environmentally realistic concentrations of hard clams (*M. mercenaria*) maintained non-bloom densities of *Aureococcus* ($\sim 10^3$ ml^{-1}), while identical mesocosms with no or few clams developed dense brown tide blooms ($>10^5$ ml^{-1}) (Cerrato et al. 2004). *Aureococcus* inhibits *M. mercenaria* grazing rates at densities above 4×10^3 cells ml^{-1}. Thus, there may be a threshold effect whereby the clams consume *Aureococcus* at low cell densities, and grazing retards bloom development, but clams are inhibited at high cell concentrations, promoting brown tide blooms (Bricelj et al. 2001).

Reduced grazing pressure appears to have been an important factor in both the initiation and persistence of the eight-year Texas brown tide bloom (Buskey and Stockwell 1993; Buskey et al. 1997). The bloom was initiated in the hypersaline upper reaches of Baffin Bay and was preceded by a period of unusually high salinities (up to 70 PSU), which greatly reduced the abundance of microzooplankton, and important benthic grazers such as the bivalve *Mulinia lateralis* (Buskey et al. 1997). The spread of the bloom to lower Baffin Bay and the Laguna Madre in June 1990 was accompanied by a large decline in both the abundance of mesozooplankton (e.g., *Acartia tonsa*), and in grazing rates of microzooplankton (Buskey and Stockwell 1993). Gut contents, growth, and egg laying in adult *Acartia* were severely reduced during the bloom, suggesting that the zooplankton were either unable to feed upon, or actively avoided *Aureoumbra* cells. Subsequent laboratory experiments verified these findings for adult *Acartia* and showed that the presence of *Aureoumbra* increased the mortality of *Acartia* nauplii relative to unfed (starved) nauplii (Buskey and Hyatt 1995). Increased concentrations of *Aureoumbra* also caused a dose-dependent increase in mortality in two microzooplankton species (the ciliate *Strombidinopsis* sp. and the rotifer *Brachionus plicatilus*). A third species was unable to grow on *Aureoumbra* and three others had reduced growth rates compared to cultures fed on equal concentrations of control algae (Buskey and Hyatt 1995). The increased mortality observed in some zooplankton species suggests the presence of a toxin, but no toxin has yet been identified (Liu and Buskey 2000). The putative toxicity of *Aureoumbra* or an inability of zooplankton to feed and grow on this algal food source likely contributed substantially to the development and persistence of the Texas brown tide bloom (Buskey and Stockwell 1993).

Viruses may influence the dynamics of *Aureococcus* blooms. Electron micrographs of the first observed brown tide event in Rhode Island and subsequent blooms in New Jersey and New York revealed the presence of intracellular, icosahedral virus-like particles in *Aureococcus* cells (Sieburth et al. 1988; Gastrich et al. 2002), suggesting that brown tide populations may experience viral infection and lysis. Virus densities during *Aureococcus* blooms are generally elevated compared to most estuarine environments (Gobler et al. 2004a) and field studies have observed a high percentage (~40 %) of virally infected *Aureococcus* cells as blooms end. Thus, viruses may be an important source of mortality during bloom termination (Gastrich et al. 2004). *Aureococcus*-specific viruses capable of completely lysing brown tide cultures have been isolated from bloom waters in Long Island estuaries (Gobler et al. 2004 c). However, these viruses infect only a portion of available clones of *Aureococcus* (Gobler et al. 2004 c). Hence, viruses may have a greater impact on bloom diversity than biomass. Thus far, only a small number of viral strains have been tested, and there may be others yet to be isolated, which can infect the *Aureococcus* clones resistant to the currently available virus strains. To date, there is no evidence for viruses that infect *Aureoumbra*.

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