Control of harmful algal blooms (HABs) specieswith a focus on Dinoflagellate

Seong-Yun Jeong[1]

[1]*Department of Biomedical Science, Daegu Catholic University, Gyeongsan 38430, Korea., Corresponding Author: Seong-Yun Jeong, Department of Biomedical Science, Daegu Catholic University, Gyeongsan 38430, Korea.*

Abstract- Algicidal microorganisms induce microalgae growth inhibition, death and subsequent lysis. Secreted algicidal molecules and enzymes produced by bacteria, cyanobacteria, viruses and the microalga themselves that are capable of inducing algal death are classified, and the known modes of action are described along with insights into cell-to-cell interaction and communication.Speciously, algicidal bacteria have been extensively used for biological termination of harmful algal blooms and red tides. Some of the bioactive molecules produced are capable of provoking microalgae hydrolysis causing growth inhibition, death and complete algal disruption. These bioactive substances or allelopathic molecules encompass chemicals, lipids, peptides and enzymes.The identified algicidal substances against microalgae include: alkaloid molecules such as derivates of quinolones, indole alkaloids, enzymes, which are mainly produced by algicidal bacteria.This review aims to provide information regarding microalgae degradation by microorganisms and secreted algicidal substances that would be useful for microalgae cell breakdown.

Keywords:Algicidal bacteria, Algicide, Dinoflagellate, harmful algal blooms

I. INTRODUCTION

Coastal regions around the world have many environmental problems, such as coastal water pollution, overfishing, extermination of marine mammals and red tides. Among that kind of marine environmental problems, red tide and fish kills can be caused by harmful algae blooms (HABs). In past decades, the HABs associated dinoflagellates have dramatically increased all over the world.Dinoflagellates exist widely in aquatic environments. Only about half of the dinoflagellate species are photosynthetic. These organisms have two whip-like appendages called flagella and they can swim short distance using the flagella. Like most single-celled algae, dinoflagellates usually reproduce by mitosis. Cells divide in two, the two into four and so on.

Concerns about HABs have increased over the last decade largely because of the effects on fisheries and the associated decline in water quality. The impacts of these blooms are felt in many ways: human health is placed at risk; ecosystems are altered; marine mammals are injured or killed; and the fishing, aquaculture, and recreation industries suffer economic losses.Research has also been carried out on algicidal organisms and bloom dynamics. However, proper and successful way to control HABs has not yet been accomplished. Since the fact that bacteria play on important role in the development and declination of HABs in the sea with physical and chemical factors was founded, many studies on algicidal bacteria have been conducted (Kim et al., 1998; Lennemanet al., 2014).

This paper reviews degradation by algicidal microorganisms as an alternative biological method for microalgal cell disruption including the recent studies applying microbial degradation. The advantages and disadvantages of this disruption method are explored and insights into cell-to-cell interaction and communication are given. A description of secreted algicidal bioactive molecules and enzymes, together with their known mechanisms of action is presented. The main aim of this study was to develop environmentally acceptable strategies for direct control in ongoing HAB events for the purpose of providing basic knowledge about eliminating toxic or harmful cells or inhibiting their growth using algicidal bacteria.

II. DEFINITION OF THE TERM 'HARMFUL ALGAL BLOOMS (HABS)'

The microscopic planktonic algae of the world's oceans are critical food source for shellfish and the larvae of crustaceans and finfish (Sarthouet al., 2005). Microalgae are beneficial for aquaculture and wild fisheries operations. However, blooms of plankton can have a negative effect (Hallegraeff, 1995). Some toxic microalgae produce toxins and kill wild and cultivated fishes. Sometimes, microalgal toxinsare accumulated in filter-feeding shellfish and have a negative impact on human activities; therefore, algal blooms so-called 'harmful algal blooms (HABs)'. The term 'red tide' is a common name of algal blooms. However, discoloration of the water might be of other various colors — white, blue, green, brown or purple — and red tide causes no negative effects, sometimes. Therefore, scientists have used the term HABs since it was introduced for the first time in 1974.

III. THE DIVERSITY OF HAB SPECIES

Non-toxic algae are not usually harmful and just generate discoloration. Even non-toxic species can be harmful when they accumulate in sufficient numbers to discolor the water, reduce of water clarity, shade submerged vegetation, disrupt food-web dynamics and cause oxygen depletion (Hallegraeff, 1995). Some noxious algae may indirectly act on marine resources. The harmful impact of noxious species are related with mechanical effects, such as gill clogging by producing mucus, lesions or necrosis while harmful algae usually affect marine organisms by producing toxins. A reduction in oxygen and hydrogen sulfide production can also cause mass mortalities of commercially valuable wild and farmed marine resources (Hallegraeff, 1995; Zingone and Enevoldsen, 2000). Toxic algae can be a little fraction of the total microalgal population but still be dangerous. Some toxic algae produce noxious toxins and the toxins impinge on human health through the food chain. The case of diarrhetic shellfish poisoning (DSP) has been reported with a few Dinophysis concentrations (100 cells/L).

Toxicity and other deleterious impact caused by harmful microalgae are not limited to a single algal class or to a few genera, even within a single species different populations of the same species may be toxic or not because of different growth and life strategies (Anderson, 1997; Gallagher, 1998).

IV. NEGATIVE EFFECTS CAUSED BY HABS

4.1 Risks for human health

Microalgal toxins have different structure or toxicity and cause more than 60,000 poisoning events annually (Gill et al., 2003). These noxious toxins accumulate gastrointestinal tract or body tissues of specific vector organisms and reach humans through food chain. The most toxic algal species are dinoflagellates, but several diatoms and cyanobacteria also produce neurotoxin that can endanger human health (Sakai et al., 2007). These toxins induce some acute and chronic syndromes. For example, paralytic shellfish poisoning (PSP), diarrhoeic shellfish poisoning (DSP), neurotoxic shellfish poisoning (NSP), amnesic shellfish poisoning (ASP), and ciguatera fish poisoning (CFP), which cause a various neurological or gastroenteric symptoms; sometimes this syndrome can be fatal (Camacho et al., 2007; Hallegraeff, 1993).

4.2 Impact on tourism and on the recreational use of coastal areas

The exploitation of tourism and recreational resources in coastal areas is a higher value-added business and has need of a high quality of the environment including unaltered seawater color, transparency. Algal blooms generate discoloration, which earned them the name of `red-tides' and intense discolorations of seawater reduce water clarity; discoloration by HABs can affect tourism and recreational use of coastal areas.

4.3 Damage to the marine ecosystem

The degradation of HABs can exhaust oxygen supplies, thus killing not only commercially important fishes, but also other shellfish, plants and animals. The biomass degradation co-occurs limiting light and disrupts food-web dynamics. Hydrogen sulfide production can also cause mass mortalities. Harmful algae usually affect marine organisms by producing toxins, producing hydrogen sulfide, and depleting oxygen (Hallegraeff, 1995; Zingone and Enevoldsen, 2000).

V. COMPLEX LIFE CYCLE OF HAB SPECIES

The eco-physiological requirements of most HAB species are inadequately known, and laboratory studies are needed to learn more about this field. However, results from laboratory studies are not adequate to applicate the life cycle of HAB species in the sea. In fact, growth of harmful species has complex interactions with other organisms which are barely reproducible in laboratory experiments; life cycle of harmful species in the real world is more complicated. Phytoplankton species have complex life cycles and alternation of stages — vegetative cell stages and resting cyst stages (Wyatt, 1997). Benthic resting stages, non-motile, are widely distributed among harmful dinoflagellates and raphidophytes. At the end of HABs, resting cyst was formed to prepare the next bloom. So, it is called the 'seed bank'.

VI. CONTROL OF HABS

Application of yellow loess and clays may be able to flocculate and remove algal cells from the water column (Choi et al., 1998; Sun et al., 2004). These methods have been found to be effective. However, yellow loess and clay cause secondary effects on bottom-dwelling organisms (Bricelj and Malouf, 1984). Chemical agents such as copper sulfate, hydrogen peroxide, and triosyn are effective in controlling blooms within a short period after application (Ryuet al., 1998), but their usage in aquatic ecosystems is potentially dangerous due to their side effects (Jeong et al., 2000).

6.1 Mechanical control method

Mechanical control implies the use of filters, pumps, and barriers to exclude HABs from impacted waters. Pumping of surface algal cells has proven be an effective method to temporarily protect freshwater lakes from exposure to cyanobacteria and aeration has also been effective in reducing cyanobacterial blooms. Filtration has been used effectively in purgation of drinking water supplies. Barrier systems might be able to block HABs, dead organisms, or other bloom-related materials from beaches, recreational areas or aquaculture sites. Sonication is also might be able to control resting cysts and algal cells in ballast water system (Holm et al., 2008).

6.2 Chemical control method

Chemical control implies the use of chemical or mineral compounds to remove HABs. Chemicals have been used to control HABs in drinking water supplies and enclosed freshwater systems. These include copper compounds, triosyn, and chemical oxidants — chlorine, peroxide, ozone, and chloramines (Oemcke and Leeuwen, 2005; Ryuet al., 1998). They are likely to kill toxic algal cells, but their usage in aquatic ecosystems is potentially dangerous because of toxins and their side effects. Attempts to use chemicals to directly control HABs need to minimize the side impacts.

6.3 Application of clay or yellow loess

Application of clays or yellow loess may be able to flocculate and remove HABs, but treatment of clay causes secondary effects on bottom-dwelling organisms (Sengcoet al., 2001; Sengco and Anderson, 2003; Beaulieu et al., 2005; Park, 2006, 2007). In Korea, clay has been used to manage HABs on a large scale in fish farms. However, application of clay has restricted due to secondary effects. Therefore, it was needed to development of new techniques that did not cause environmental impacts.

VII. ALGICIDAL BACTERIA

Bacteria have significant impacts on aquatic biogeochemical processes such as carbon flux and nutrient regeneration (Azam, 1998; Doucette et al., 1998; Copley, 2002). Specifically, a bacterial assemblage can have inhibitory or stimulatory effects on algal growth during a bloom event (Amaroet al., 2005; Fukamiet al., 1997; Simon et al., 2002). Doucette et al. (1999) hypothesized that the relative and absolute abundances of algicidal bacteria, in particular, would increase as a bloom moves through its initiation, development, and maintenance phases. Ultimately, changes in the abundance and composition of the bacterial community may lead to bloom decline as these algicidal bacteria begin to negatively impact algal growth and/or render the alga more susceptible to other factors, such as grazing pressure and nutrient competition (Lewituset al., 2003; Bunker, 2004; Liu et al., 2008). The extent to which bloom termination is a reflection of bacterially mediated algal lysis remains unknown.

According to Zhou et al. (2014), 95% of these algicide bacteria belong to gram-negative bacteria with 50% from the Cytophaga–Flavobacteria–Bacteroidetes (CFB) group and about 45% from γ-Proteobacteria such as Alteromonas, Pseudomonas and Pseudoalteromonas. The remaining 5% are members of the gram-positive bacteria from the Firmicutes (Bacillus) and Actinobacteria phyla, genera Micrococcus and Planomicrobium.Although there is no conclusive link between phylogeny and the lytic mechanism, the available data suggest that gram-positive bacteria and γ-Proteobacteria employ primarily an indirect mode of attack, while the lytic activity of the CFB group can involve either direct or indirect interactions with target cells (Mayali and Azam, 2004; Rho et. al., 2008; Salomon and Imai, 2006). Although the functional significance of cell lysis by algicidal bacteria remains to be determined, this activity clearly enhances the supply of algal-derived organic nutrients that may then provide a competitive advantage to this segment of the microbial community (Mayali and Azam, 2004; Rho et. al., 2008).

7.1 Degradation by microorganisms for microalgal cell disruption

Algicidal bacteria and viruses have been extensively used for biological termination of harmful algal blooms and red tides (Bai et al., 2012;Mayali and Azam, 2004). This phenomenon is usually referred to as allelopathy. These natural defense mechanisms occur between a microorganism and its predator, parasite. Furthermore, allelopathic interaction between bacteria and microalgae have recently been highlighted as a potential strategy to control culture contamination during algal cultivation (Bacellar Mendes and Vermelho, 2013), to fast-sedimentation of microalgae by bacterial aggregation (Wang et al., 2014) and to disrupt microalgae using algicidal microorganisms (Lennemanet al., 2014).

Mayali and Doucette (2002) demonstrated that bacterial assemblages associated to algal cultures are able to confer resistance or susceptibility to algicidal attack by bacteria, and is not an intrinsic property of the algal strain. Algicidal bacteria not only interact with targeted algal species, but also with the ambient microbial community (Nagasaki et al., 2000; Roth et al., 2008). This finding indicates the complexity and importance of microbial interactions. Therefore, the algicide activity effect should be carefully examined in various microbial assemblages to develop the biological control of eukaryotic algae using bacteria.

Most known alga-lytic bacteria are directed against diatoms, dinoflagellates and raphidoflagellates. Due to the extent of studies in algal bloom terminations, much is known about the mode of action of bacterial lysis and the types of allelochemical or enzymes secreted by the algicidal bacteria. In many cases, these alga-lytic bacteria are genus- or species-specific and their abundance has been shown to increase during the decline of algal population (Kim et al., 2007). Approximately 70% of the interaction takes place through an indirect attack, whereas 30% requires direct cell contact (Zhou et al. Dinoflagellate, 2014). Nevertheless, the overall effectiveness of algicidal attack does not appear to be influenced by whether or not contact with algal cells occurs (Roth et al., 2008). However, it is noteworthy to mention that direct cell contact affected algae cell morphology and induced cell lysis more rapidly than an indirect attack (Roth et al., 2008).

Direct cell-to-cell contact is mainly needed for some bacterial phyla such as Cytophaga sp., Flavobacterium sp. and Saprospira sp. to attack and lyse alga cells (Lennemanet al., 2014). Bacterial cell-to-algal cell interaction occurs according to a characterized bacterial behavior.

7.2 Indirect attack by releasing extracellular compounds.

Some of the bioactive molecules produced are capable of provoking microalgae hydrolysis causing growth inhibition, death and complete algal disruption. These bioactive substances or allelopathic molecules encompass chemicals, lipids, peptides and enzymes. They are commonly secreted by macroalga (Goeckeet al., 2010), microalga (Leflaive and Ten-Hage, 2007), cyanobacteria, bacteria (Zhou et al., 2014) and viruses (Bai et al., 2012).In this approach, alga-lytic enzymes or allelochemicals are secreted by the co-cultured microorganisms leading to a strain and cell wall-specific lysis of microalgae. They have been collected from the natural environment of marine microalgae in order to reach cell lysis in saline conditions (Lenneman et al., 2014) or isolated from environmental samples recovered in contaminated sediments (Lennemanet al., 2014). Specific microalgae cell wall damage showed evidence of the effectiveness of biological treatment (Lennemanet al., 2014). One of the major reasons for the damage to microalgal cell wall was reported to be the enzymatic degradation, which was confirmed by the detection of enzymatic activities in co-culture supernatants (Muñoz et al., 2014). The bacterial attack and induced cell lysis, showed some degree of selectivity and specificity for a certain species of microalgae according to their mobility and cell wall thickness and rigidity (Lennemanet al., 2014).

Alga-lytic microorganisms encompass bacteria, cyanobacteria, microalga themselves and viruses. They mainly act through an indirect attack and kill the targeted algae by releasing extracellular allelopathic compounds.Microalgae growth inhibition and lysis are regulated in a dose-dependent manner by cell density and/or by the amount of compound released. The secretion of these substances is always found to require a minimum cell density relative to late exponential phase or early stationary phase (Roth et al., 2008).The allelopathic activity of secreted compounds and mode of action depends on the nature of the compound released and varies according to the targeted microalgae strain, cell wall rigidity and composition.

In the case of Saprospira sp. SS98-5 and Aquimarina sp. strain antisso-27, cell lytic activities have been shown to be related to enzymatic activity abilities (Chen et al., 2012).Saccharophagusdegradans strain BS03 has been referred to as strong algicidal bacterium (Fu et al., 2012). Different effects of algicidal activity were detected including the decrease of chlorophyll a, inhibition of photosynthesis, inhibition of antioxidant enzymes activities, the increase in malodialdehyde content, the increase in caspase-3 protease activities and the increase of lipid peroxidation of the algal membrane (Fu et al., 2012).

7.3 Microalgae cell disruption by algicidal substances or algicide

The identified algicidal substances against microalgae include: alkaloid molecules such as derivates of quinolones (Cho, 2012), indole alkaloids (Yang et al., 2015), enzymes (Cheng et al., 2013), which are mainly produced by algicidal bacteria. The effectiveness of these algicides is determined in a concentration-dependent manner.

The prodigiosin is a natural red pigment that belongs to a large family of linear tripyrrolyl antibiotics. It is a well-known natural algicidal product of marine γ-proteobacteria such as Hahellachejuensis, Pseudoalteromonas, Serratia sp. and Vibrio sp. (Kim et al., 2008). The dinoflagellate Cochlodinium polykrikoides treated with prodigiosin displayed morphological changes, intracellular leakage and rapid cell lysis. Some other indole alkaloids that have been found to be potent algicidal molecules, include Bacillamide, a 2-Acetyl-N-[2-(1H-indol-3-yl)ethyl]-1,3-thiazole-4-carboxamide produced by Bacillus sp. SY1 (Jeong et al., 2003), and 2,3-indolinedione (isatin) produced by Pseudomonas sp. C55a-2 (Sakata et al., 2011).

Another example of the algicidal efficiency is the one of 19-residue amphipathic α-helical peptide HP and its analogs HPA3 and HPA3NT3 (Park et al., 2011). They have been isolated from the N-terminal region of the H.

pylori ribosomal protein, L1. They have been shown to exert potent algicidal activity and to display a rapid lysis action in only 2 min against raphidoflagellates, and 1 h against dinoflagellates in a strain-specific way (Park et al., 2011).Wang et al. (2005) described an algicidal glycolipid produced by Pseudomonas aeruginosa. This is a biosurfactant composed of l-rhamnose and 3-hydroxyalkanoic acid and named rhamnolipid. Rhamnolipid was able to induce severe damage on the plasma membrane of algae which partly disintegrated (Wang et al., 2005). Additionally, a set of extracellular enzymes produced by Cytophaga sp. has been described as responsible for the cellular lysis of a dinoflagellate. These enzymes have been determined as aminopeptidase, lipase, glucosaminidase and alkaline phosphatase (Amaroet al., 2005).

The degradation of microalgae using algicidal microorganisms in co-cultures has recently been employed to induce microalgae cell disruption. It is noteworthy that inter-and intra-species cell-to-cell communication do not have to be neglected. Further investigations should focus on understanding inter-species communication and the induction and regulation of defense mechanisms. More insights are needed about specific mechanisms of algal cell lysis in the order to describe how the disruption process takes place. However, based on literature, lysis efficiency seems to be regulated by algicidal microorganism density and algicide concentration. Algicidal enzyme could also be produced by a more suitable micro-organism for a co-culture, or directly by microalgae. Secreted algicide compounds and enzymes could be used to develop new microalgal lytic systems

VIII. CONCLUSION

With the increasing interest in using microalgal biomass, new cost-effective cell disruption methods require development to overcome the problems. Microalgal degradation by algicidal microorganisms has already been employed to induce cell lysis. Microalgae cell lysis provoked by natural and biodegradable algicidal allelochemicals and secreted enzymes are non-toxic for the environment and species- or strain-specific. Therefore, algicidal microorganisms and their algicides are promising and potentially more environmentally sustainable tools in the marine eco-systems. A better understanding of alga-bacteria interaction and of the specific mechanisms of algal cell lysis is expected to be an important breakthrough to reduce the cost of microalgae cell disruption.

IX. REFERENCES

[1] Amaro, A.M., M.S. Fuentes, S.R. Ogalde, J.A. Venegas, and B.A. Suárez-Isla. 2005. Identification and characterization of potentially algal-lytic marine bacteria strongly associated with the toxic dinoflagellate Alexandrium catenella. J. Eukaryot. Microbiol.52, 191-200.

[2] Anderson, D.M. 1997. Turning back the harmful red tide.Nature 38, 513–514

[3] Azam, F. 1998. Microbial control of oceanic carbon flux: The plot thickens. Science 280, 694–696.

[4] Bacellar Mendes, L.B. and A.B. Vermelho. 2013. Allelopathy as a potential strategy to improve microalgae cultivation. Biotechnol.Biofuels.6, 152.

[5] Bai, S., H. Wang, and T. Zheng. 2012. Marine algal viruses and their application in red-tide control. Chinese J. Appl. Environ. Biol. 18, 1056-1065.

[6] Beaulieu, S.E., M.R. Sengco, and D.M. Anderson. 2005. Using clay to control harmful algal blooms: deposition and resuspension of clay/algal flocs. Harmful Algae 4, 123–138.

[7] Bricelj, V.M. and R.E. Malouf. 1984. Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam Mercenariamercenaria. Mar. Biol. 84, 155–165.

[8] Bunker, K.N. 2004.A hydrologic assessment of two detention pond watersheds in an urban coastal landscape. M. Sc. Thesis. Masters in Environmental Studies, The Graduate School, College of Charleston.

[9] Camacho, F.G., J.G. Rodríguez, A.S. Mirón, M.C.C. García, E.H. Belarbi, Y. Chisti, and E.M. Grima. 2007. Biotechnological significance of toxic marine dinoflagellates. Biotechnol.Advan.25, 176–194.

[10] Chen, W.M., F.S. Sheu, and S.Y. Sheu. 2012. Aquimarinasalinaria sp. nov., a novel algicidal bacterium isolated from a saltpan. Arch. Microbiol. 194, 103-112.

[11] Cheng, Y.S., Y. Zheng, J.M. Labavitch, and J.S. VanderGheynst. 2013. Virus infection of Chlorella variabilis and enzymatic saccharification of algal biomass for bioethanol production. Bioresour. Technol. 137, 326-331.

[12] Cho, J.Y. 2012.Algicidal activity of marine Alteromonas sp. KNS-16 and isolation of active compounds.Biosci.Biotechnol.Biochem. 76, 1452-1458.

[13] Choi, H.G., P.J. Kim, W.C. Lee, S.J. Yun, H.G. Kim, and H.J. Lee. 1998. Removal efficiency of Cochlodinium polykrikoides by yellow loess. J. Kor. Fish. Soc. 31, 109–113.

[14] Copley, J. 2002. All at sea.Nature 415, 572–574.

[15] Doucette, G.J., M. Kodama, S. Franca, and S. Gallacher. 1998. Bacterial interactions with harmful algal bloom species: bloom ecology, toxigenesis, and cytology. p. 619–647. In: Anderson, D., Cembella, A.D., Hallegraeff, G.M. (eds.), Physiological Ecology of Harmful Algal Blooms, G 41. Springer-Verlag, Berlin, Heidelberg, Germany.

[16] Doucette, G.J., E.R. McGovern, and J.A. Babinchak. 1999. Algicidal bacteria active against Gymnodinium breve (Dinophyceae). I. Bacterial isolation and characterization of killing activity. J. Phycol. 35, 1447–1454.

[17] Fu, L., D. Li, C. Wu, and T. Zheng 2012.Effects of algicidal bacterium BS03 (Microbulbifer sp.) on the growth and antioxidant systems of Alexandrium tamarense.ActaMicrobiol.Sin. 52, 784-790.

[18] Fukami, K., T. Nishijima, and Y. Ishida. 1997. Stimulative and inhibitory effects of bacteria on the growth of microalgae. Hydrobiologia 358, 185–191.

[19] Gallagher, J.C. 1998. Genetic variation in harmful algal bloom species: an evolutionary ecology approach. p. 225–242. In: Anderson D.M., Cembella A.D., Hallegraeff G.M. (eds.), Physiological ecology of harmful algal blooms. Springer, Berlin, Germany.

[20] Gill, S., M. Murphy, J. Clausen, D. Richard, M. Quilliam, S. MacKinnon, P. LaBlanc, R. Mueller, and O. Pulido. 2003. Neural injury biomarkers of novel shellfish toxins, Spirolides: A pilot study using immunochemical and transcriptional analysis. NeuroToxicology24, 593–604.
[21] Goecke, F., A. Labes, J. Wiese, and J.F. Imhoff. 2010. Review chemical interactions between marine macroalgae and bacteria. Mar. Ecol. Prog. Ser. 409, 267-300.
[22] Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase.Phycologia 32, 79–99.
[23] Hallegraeff, G.M. 1995. Harmful algal blooms: A global overview. p. 1–22. In: Hallegraeff G.M., Andeson D.M., Cembella A.D. (eds.), Manual on harmful marine microalgae, UNESCO, Paris, France.
[24] Holm, E.R., D.M. Stamper, R.A. Brizzolara, L. Barnes, N. Deamer, and J.M. Burkholder. 2008. Sonication of bacteria, phytoplankton and zooplankton: Application to treatment of ballast water. Mar. Pollut. Bull. 56, 1201–1208.
[25] Jeong, J.H., H.J. Jin, C.H. Sohn, K.H. Suh, and Y.K. Hong. 2000. Algicidal activity of the seaweed Corallinapilulifera against red tide microalgae. J. Appl. Phycol. 12, 37–43.
[26] Jeong, S.Y., K. Ishida, Y. Ito, S. Okada, and M. Murakami. 2003. Bacillamide, a novel algicide from the marine bacterium, Bacillus sp. SY-1, against the harmful dinoflagellate, Cochlodinium polykrikoides. Tet.Lett. 44, 8005–8007.
[27] Kim, J.D., B. Kim, and C.G. Lee. 2007. Alga-lytic activity of Pseudomonas fluorescens against the red tide causing marine alga Heterosigma akashiwo (Raphidophyceae). Biol. Control. 41, 296-303.
[28] Kim, D., J.F. Kim, J.H. Yim, S.K. Kwon, C.H. Lee, and H.K. Lee. 2008. Red to red — the marine bacterium Hahellachejuensis and its product prodigiosin for mitigation of harmful algal blooms. J. Microbiol. Biotechnol. 18, 1621-1629.
[29] Leflaive, J., and L. Ten-Hage. 2007. Algal and cyanobacterial secondary metabolites in freshwaters: a comparison of allelopathic compounds and toxins. Freshwat. Biol. 52, 199-214.
[30] Lenneman, E.M., P. Wang, and B.M. Barney. 2014. Potential application of algicidal bacteria for improved lipid recovery with specific algae. FEMS Microbiol.Lett. 354, 102-110.
[31] Lewitus A.J., L.B. Schmidt, L.J Mason, J.W. Kempton, S.B. Wilde, J.L. Wolny, B.J. Williams, K.C. Hayes, S.N. Hymel, C.J. Keppler, and A.H. Ringwood. 2003. Harmful algal blooms in South Carolina residential and golf course ponds. Popul. Environ. 24, 387–413.
[32] Liu, J., A.J. Lewitus, J.W. Kempton, and S.B. Wilde. 2008. The association of algicidal bacteria and raphidophyte blooms in South Carolina brackish detention ponds. Harmful Algae 7, 184–193.
[33] Mayali, X., and G.J. Doucette. 2002. Microbial community interactions and population dynamics of an algicidal bacterium active against Karenia brevis (Dinophyceae). Harmful Algae. 1, 277-293.
[34] Mayali, X. and F. Azam. 2004. Algicidal bacteria in the sea and their impact on algal blooms. J. Eukaryot. Microbiol. 51, 139–144.
[35] Muñoz, C., C. Hidalgo, M. Zapata, D. Jeison, C. Riquelme, and M. Rivas. 2014. Use of cellulolytic marine bacteria for enzymatic pretreatment in microalgal biogas production. Appl. Environ. Microbiol. 80, 4199-4206.
[36] Nagasaki, K., M. Yamaguchi, and I. Imai. 2000. Algicidal activity of a killer bacterium against the harmful red tide dinoflagellate Heterocapsacircularisquama isolated from Ago Bay. Japan. Fish. Sci. 66, 666-673.
[37] Oemcke, D.J. and J. Hans van Leeuwen 2005.Ozonation of the marine dinoflagellate alga Amphidinium sp.—implications for ballast water disinfection. Water Res.39, 5119–5125.
[38] Park, S.C., J.K. Lee, S.W. Kim, and Y. Park. 2011. Selective algicidal action of peptides against harmful algal bloom species. PLoS One.6, Article e26733.
[39] Rho, P.B., M.J. Twiner, C.M. Mikulski, A.B. Barnhorst, and G.J. Doucette. 2008. Comparative analysis of two algicidal bacteria active against the red tide dinoflagellate Karenia brevis. Harmful Algae 7, 682–691.
[40] Roth, P.B., M.J. Twiner, C.M. Mikulski, A.B. Barnhorst, and G.J. Doucette. 2008. Comparative analysis of two algicidal bacteria active against the red tide dinoflagellate Karenia brevis. Harmful Algae. 7, 682-691.
[41] Ryu, H.Y., J.M. Shim, J.D. Bang, and C. Lee. 1998. Experimental chemical treatments for the control of dinoflagellate, Cochlodinium polykrikoides in the land-based culture of olive flounder Paralichthysolivaceus. Kor. J. Aquacult. 11, 285–294.
[42] Sakai, H., K. Oguma H. Katayama, and S. Ohgaki. 2007. Effects of low or medium-pressure UV irradiation on the release of intracellular microcystin. Water Research 41, 3458–3464.
[43] Sakata, T., T. Yoshikawa, and S. Nishitarumizu. 2011. Algicidal activity and identification of an algicidal substance produced by marine Pseudomonas sp. C55a-2. Fish. Sci. 77, 397-402.
[44] Sarthou, G., K.R. Timmermans, S. Blain, and P. Tréguer. 2005. Growth physiology and fate of diatoms in the ocean: a review. J. Sea Res. 53, 25–42.
[45] Sengco, M.R., A. Li, K. Tugend, D. Kulis, and D.M. Anderson. 2001. Removal of red- and brown-tide cells using clay flocculation. I. Laboratory culture experiments with Gymnodinium breve and Aureococcusanophagefferens. Mar. Ecol. Prog. Ser. 210, 41–53.
[46] Sengco, M.R. and D.M. Anderson. 2003. 147 Controlling harmful algal blooms through clay flocculation. J. Phycol. 39, 51–51.
[47] Wang, X., L. Gong, S. Liang, X. Han, C. Zhu, and Y. Li. 2005.Algicidal activity of rhamnolipidbiosurfactants produced by Pseudomonas aeruginosa.Harmful Algae. 4, pp. 433-443
[48] Wyatt, T. and I.R. Jenkinson. 1997. Notes on Alexandrium population dynamics. J. Plankton Res. 19, 551–75.
[49] Yang, Q., L. Chen, X. Hu, L. Zhao, P. Yin, and Q. Li. 2015. Toxic effect of a marine bacterium on aquatic organisms and its algicidal substances against Phaeocystisglobosa.PLoS One. 10.
[50] Zhou, J., G.F. Chen, X.S. Zhu, L. Chen, and Z.H. Cai. 2014. A review of the relationship between algae and bacteria in harmful algal blooms. Acta Ecol. Sin. 34, 269-281.
[51] Zingone, A. and H.O. Enevoldsen. 2000. The diversity of harmful algal blooms: a challenge for science and management. Ocean Coast.Manag. 43, 725–748.