Interactions between marine bacteria and red tide organisms in Korean waters

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There is increasing interest in the relationships between marine bacteria and red tide organisms. Some bacteria are known to kill red tide organisms, and may be responsible for accelerating the termination of red tides. Thus, certain algicidal bacteria have been proposed for the control of red tides. Meanwhile, many red tide organisms are known to feed on marine bacteria. The roles of marine bacteria and red tide organisms are therefore reversible. In Korean waters, the killing of red tide organisms by algicidal bacteria, and also the feeding of red tide organisms on marine bacteria have been extensively investigated. The findings of such studies may influence the conventional view of red tide dynamics, and also planktonic food webs. Here, we review the species and concentrations of algicidal bacteria that kill red tide organisms in Korean waters, as well as the ingestion rate and grazing impact of red tide organisms on marine bacteria. Furthermore, we offer an insight into the ecological roles of these 2 components in marine planktonic food webs.

Key Words: algicidal bacteria; feeding; food web; graze; harmful algal bloom; red tide; trophic interaction

INTRODUCTION

Red tides—discoloration of the surface of the sea due to the blooms of plankton—constitute one of the most important environmental issues globally. By altering the balance of food webs and causing large-scale mortalities of fish and shellfish, red tides often lead to considerable losses in the aquaculture and tourist industries (Whyte et al. 2001, Curtiss et al. 2008, Richlen et al. 2010, Jeong and Kang 2013, Park et al. 2013c). Thus, many countries are endeavoring to understand the process of red tides, and thereby predict and control their outbreaks (e.g., Mackey et al. 1996). Red tide dynamics are known to be influenced by diverse physical, chemical, and biological properties (Cole 1982, Doucette et al. 1998, Imai et al. 2001, Han et al. 2010, Tang and Gobler 2010, Jeong et al. 2013a, 2013b, Kang et al. 2013, Kim et al. 2013a, 2013b, Lee et al. 2013, Park et al. 2013b, Yih et al. 2013, Yoo et al. 2013).

Several investigations have revealed that certain bacteria kill red tide organisms, thereby playing an important role in the decline of red tides (Imai et al. 1993, 2001, Doucette et al. 1998, Salomon and Imai 2006). Thus, the killing of red tide organisms by algicidal bacteria has been extensively studied (Fukami et al. 1992, Mayali and Doucette 2002). Meanwhile, in the last 2 decades, many red tide organisms, including phototrophic dinoflagellates and raphidophytes, have been shown to feed on bacteria (Nygaard and Tobiensen 1993, Seong et al. 2006, Jeong et al. 2010a, 2010b, 2010c, Jeong 2011, Park et al. 2013a). The predator-prey relationships of red tide organisms and bacteria (2 major components of marine environments) are therefore reversible.
In Korea, red tides have led to considerable losses in the aquaculture industries (Park et al. 2013c). Thus, methods to control the outbreak and persistence of red tides, and thereby reduce their economic impacts, are urgently required. Several potential control methods have been suggested or implemented (Jeong et al. 2002, 2003a, 2008, Sengco and Anderson 2004, Park et al. 2013c), including the use of mass-cultured algicidal bacteria.

Here, we review the species and concentrations of algicidal bacteria that kill red tide organisms in Korean waters, as well as the ingestion rates and grazing impact of red tide organisms on bacteria. Furthermore, we examine the ecological significance of the interactions between these 2 components of marine environments.

**BACTERIA AS KILLERS OF RED TIDE ORGANISMS IN KOREAN WATERS**

**Species of algicidal bacteria isolated from Korean waters**

Many bacteria are known to kill red tide organisms in Korean waters (Table 1). In particular, algicidal bacteria that kill the mixotrophic dinoflagellate *Cochlodinium polykrikoides*, which causes considerable great losses in the Korean aquaculture industry, have been extensively studied (Jeong et al. 2004, 2008, Park et al. 2013c). Such bacteria include *Alteromonas* sp. strain A14, *Alteromonas* sp., *Bacillus* sp. SY-1, *Hahella chejuensis* KCTC 2396, *Micrococcus* sp. LG-5, *Micrococcus luteus* SY-13, *Nautella* sp., *Pseudoalteromonas* sp. LG-2, *Pseudoalteromonas* sp., *Sagittula* sp., *Thalassobius* sp., and *Vibrio parahaemolyticus* (Table 1). The algicidal components of these bacteria were revealed to be Bacillamide and Prodigiosin (Jeong et al. 2003b, 2005). In addition, algicidal activity usually peaked at 15 hours and was subsequently maintained (Park et al. 1998, 1999, Jeong et al. 2003b, Oh et al. 2011).

The bacterium *Pseudoalteromonas haloplanktis* was shown to lyse the cell wall of another mixotrophic dinoflagellate, *Prorocentrum minimum*; the algicidal activity was revealed to be caused by the release of β-glucosidase (Kim et al. 2009a). Furthermore, *Pseudoalteromonas* sp. LG-2 was shown to kill the mixotrophic dinoflagellate *Prorocentrum micans* (Table 1). In addition, *Pseudoalteromonas fluorescens* and *Kordia algicida* OT-1 are known to kill the raphidophyte, *Heterosigma akashiwo*, while *Bacillus* sp. is known to kill another raphidophyte, *Chattonella marina*. *Bacillus* sp. was also shown to kill the mixotrophic dinoflagellates *Akashiwo sanguinea* and *Scrippsiella trochoidea*, and the raphidophytes *Fibrocapsa japonica* and *H. akashiwo* (Table 1).

*Pseudoalteromonas* sp. LG-2 killed *Prorocentrum micans*, but did not kill *Alexandrium tamarense*, *Akashiwo sanguinea*, *Cochlodinium polykrikoides* (Lee and Park 1998). In addition, *Pseudoalteromonas haloplanktis* killed *Prorocen-

**Table 1. Algicidal bacteria and target red tide organisms isolated from the Korean waters, and lowest concentrations of algicidal bacteria required to kill red tide organisms (LCBK)**

<table>
<thead>
<tr>
<th>Target red tide organism</th>
<th>Algicidal bacteria</th>
<th>LCBK (bacteria cells mL‒1)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cochlodinium polykrikoides</em></td>
<td><em>Alteromonas</em> sp. strain A14</td>
<td>9.0 × 10⁷</td>
<td>Lee et al. (2008)</td>
</tr>
<tr>
<td><em>Bacillus</em> sp. SY-1</td>
<td>Jeong et al. (2003b)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hahella chejuensis</em> KCTC 2396</td>
<td>Jeong et al. (2005)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Micrococcus luteus</em> SY-13</td>
<td>4.4 × 10⁴</td>
<td>Kim et al. (2008)</td>
<td></td>
</tr>
<tr>
<td><em>Micrococcus</em> sp. LG-5</td>
<td>1.0 × 10⁴</td>
<td>Jeong et al. (2000a)</td>
<td></td>
</tr>
<tr>
<td><em>Micrococcus</em> sp. LG-2</td>
<td>1.3 × 10⁶</td>
<td>Jeong et al. (2000b)</td>
<td></td>
</tr>
<tr>
<td><em>Vibrio parahaemolyticus</em></td>
<td>8.8 × 10⁵</td>
<td>Seong and Jeong (2011)</td>
<td></td>
</tr>
<tr>
<td><em>Prorocentrum micans</em></td>
<td>1.0 × 10⁴</td>
<td>Jeong et al. (2000b)</td>
<td></td>
</tr>
<tr>
<td><em>Pseudoalteromonas haloplanktis</em></td>
<td>1.3 × 10⁶</td>
<td>Lee and Park (1998)</td>
<td></td>
</tr>
<tr>
<td><em>P. minimum</em></td>
<td>2.5 × 10⁵ cfu mL⁻¹</td>
<td>Kim et al. (2009a)</td>
<td></td>
</tr>
<tr>
<td><em>Heterosigma akashiwo</em></td>
<td>1.0 × 10⁵</td>
<td>Jeong et al. (2000a)</td>
<td></td>
</tr>
<tr>
<td><em>Micrococcus</em> sp. LG5</td>
<td>1.0 × 10⁵</td>
<td>Kim et al. (2007)</td>
<td></td>
</tr>
<tr>
<td><em>Pseudoalteromonas fluorescens</em></td>
<td>1.0 × 10⁵ cfu mL⁻¹</td>
<td>Kim et al. (2009b)</td>
<td></td>
</tr>
<tr>
<td><em>Chattonella marina</em></td>
<td><em>Bacillus</em> sp.</td>
<td>Kim et al. (2008)</td>
<td></td>
</tr>
<tr>
<td><em>Chattonella</em> sp.</td>
<td><em>Micrococcus luteus</em> SY-13</td>
<td>Kim et al. (2008)</td>
<td></td>
</tr>
<tr>
<td><em>Eutreptiella gymnastica</em></td>
<td><em>Micrococcus</em> sp. LG5</td>
<td>1.0 × 10⁵</td>
<td>Jeong et al. (2000b)</td>
</tr>
<tr>
<td><em>Skeletonema costatum</em></td>
<td><em>Pseudoalteromonas</em> sp. A28</td>
<td>Lee et al. (2000)</td>
<td></td>
</tr>
</tbody>
</table>
trum minimum and P. donghaiense, but did not kill A. sanguinea, A. tamarense, C. polykrikoides, Gymnodinium catenatum, and Heterosigma akashiwo (Kim et al. 2009a). However, Micrococcus sp. LG-5 killed diverse algae such as C. polykrikoides, H. akashiwo, P. micans, and the euglenophyte Eutreptiella gymnastica (Jeong et al. 2000a, 2000b). Thus, some algicidal bacteria kill specific species of red tide organisms, while others kill a diverse range of red tide organisms.

On the basis the results of laboratory and field experiments, methods to control red tides using mass-cultured algicidal bacteria have been developed (e.g., Kim et al. 2009a). The efficiency of these methods requires the determination of the minimum concentrations of algicidal bacteria. In addition, the efficacy in mesocosms and natural environments must be evaluated.

**Lowest concentrations of algicidal bacteria required to kill red tide organisms isolated from Korean waters**

The lowest concentrations of algicidal bacteria required to kill target red tide organisms (LCBK) differ depending on the species of bacteria and red tide organisms (Table 1). For example, the LCBK of Micrococcus luteus SY-13 on C. polykrikoides was 3.7 × 10^3 cells mL^-1, whereas those of Vibrio parahaemolyticus, Micrococcus sp. LG-1, and Alteromonas sp. A14 ranged from 0.9 × 10^6 to 1.3 × 10^6 cells mL^-1 (Table 1). In addition, the LCBKs of Pseudomonas sp. LG-2 and Micrococcus sp. LG-5 on P. micans were 1.3 × 10^3 and 1.0 × 10^6 cells mL^-1, respectively. Thus, before using the control methods in natural environments, the LCBK must be determined.

**Mesocosms testing of algicidal bacteria for killing red tide organisms in Korean waters**

The use of algicidal bacteria to kill red tide organisms has frequently been investigated by means of field mesocosms (Kim et al. 2009a). For example, in mesocosms containing P. minimum red tide water, P. haloplanktis AFMB-08041 was found to reduce the concentration of P. minimum from 1.5 × 10^3 to 2.3 × 10^3 cells mL^-1 over 5 days (Kim et al. 2009a). Similarly, the algicidal bacterium Micrococcus sp. LG-1 (when applied at a concentration of 10^6 to 10^7 cells mL^-1) reduced the concentration of C. polykrikoides from 4.8 × 10^3 to 2.0 × 10^3 cells mL^-1 in Masan Bay (Park et al. 1998). However, before applying the method in large-scale field studies, it is important to investigate possible secondary effects on non-target organisms.

**BACTERIA AS PREY FOR RED TIDE ORGANISMS IN KOREAN WATERS**

**Type of predator**

**Mixotrophic red tide dinoflagellates.** Mixotrophic red tide dinoflagellates isolated from Korean waters are known to feed on bacteria (Table 2). For example, Amphidinium carterae, Alexandrium catenella, A. tamarense,
Ingestion and clearance rates measured in the laboratory. Seong et al. (2006) reported that an increase in the initial bacterial prey concentration to ca. $5 \times 10^6$ to $10 \times 10^6$ cells mL$^{-1}$ led to a rapid increase in the ingestion rates by *H. rotundata*, *H. triqueta*, *P. minimum*, and *C. polykrikoides*. At higher prey concentrations, the ingestion rates increased slowly or reached saturation (Fig. 1). The maximum ingestion rates ranged from 6.0 to 21.9 cells alga$^{-1}$ h$^{-1}$ (Table 2, Fig. 1). Seong et al. (2006) further reported that the maximum bacterial ingestion rates of 8 red tide algae were not significantly affected by algal size, indicating that the ingestion rates of bacteria may not be determined by the size of red tide algae.

The maximum bacterial clearance rates by red tide algae were 1.0-2.3 nL alga$^{-1}$ h$^{-1}$ for *H. rotundata*, *H. triqueta*, *P. minimum*, and *C. polykrikoides* (Table 2). These rates are comparable with those of heterotrophic nanoflagellates (HNF, 1.0-4.0 nL alga$^{-1}$ h$^{-1}$) (Eccleston-Parry and Leadbeater 1994, Zubkov and Sleigh 1995), but lower than those for ciliates (50-560 nL alga$^{-1}$ h$^{-1}$) (McQuaid 1988). Carbon acquisition from bacterial prey. Seong et al. (2006) reported that the smallest red tide alga, *Heterocapsa rotundata*, was able to acquire 76% of its daily body carbon intake from bacteria. The corresponding daily carbon acquisition by *P. minimum* was 27.1%. These data indicate that bacteria may support positive growth of small red tide dinoflagellates, with the formation of red tide alga.

![Fig. 2](http://dx.doi.org/10.4490/algae.2013.28.4.297)
tide patches. Carbon acquisition by *H. rotundata* from bacterial prey exceeds that of the heterotrophic dinoflagellate *Oxyrrhis marina*, which has the highest value among heterotrophic dinoflagellates (Fig. 2). Seong et al. (2006) further reported that bacteria may not support the growth of the large red tide algae *Heterocapsa triqueta* and *Coeloclinium polykrikoides*, which can obtain <4% of their daily body carbon intake from bacteria. Calculations of carbon acquisition and maximum volume-specific clearance rates by *H. triqueta* and *C. polykrikoides* indicated that bacteria are not suitable as the sole growth source for these large dinoflagellates, but may be considered as supplementary prey.

**Ingestion rates measured in the field.** Seong et al. (2006) reported that the mean ingestion rates of natural bacterial populations by mixotrophic red tide dinoflagellates in Korean coastal waters ranged from 1.2 to 20.6 bacteria alga⁻¹ h⁻¹ for *H. rotundata*, *H. triqueta*, *P. minimum*, *P. triestinum*, and *C. polykrikoides*. In comparison, those of HNFs and ciliates ranged from 0.7 to 39.4 bacteria HNF¹ h⁻¹ and from 15 to 713 bacteria ciliate⁻¹ h⁻¹, respectively. In contrast, the grazing coefficient of natural bacterial populations by all mixotrophic red tide dinoflagellates (0.012-1.146 d⁻¹) was significantly greater than those by all HNFs (0.008-0.196 d⁻¹) or all ciliates (0.000-0.716 d⁻¹).

*H. rotundata* / *H. triqueta*, *P. minimum* / *P. triestinum*, and *C. polykrikoides* were the most effective or the second most effective protistan predators of marine bacteria among the dominant red tide dinoflagellates, HNFs, and ciliate predators (Seong et al. 2006).

**Mixotrophic red tide raphidophytes**

The mixotrophic red tide raphidophytes *Chattonella*, *Heterosigma*, and *Fibrocapsa* isolated from Korean waters are known to feed on heterotrophic bacteria (Table 2). The maximum ingestion rates of *Heterosigma akashiwo* and *Chattonella ovata* on heterotrophic bacteria in the predators’ cultures were 11.7 and 24.5 cells alga⁻¹ h⁻¹, respectively (Table 2). Seong et al. (2006) reported that *H. akashiwo* was able to acquire 12.5% of its daily body carbon from bacteria, while *C. ovata* can obtain <4% of their daily body carbon. These data indicate that bacteria may support positive growth of *H. akashiwo*, but bacteria may be considered as supplementary prey for *C. ovata*.

Seong et al. (2006) reported that the ingestion rate of *Heterosigma akashiwo* on natural bacteria in Korean waters ranged from 2.7 to 9.0 cells alga⁻¹ h⁻¹ and the grazing coefficient of natural bacterial populations by *H. akashiwo* ranged from 0.020 to 0.867 d⁻¹. Thus, *H. akashiwo* may sometimes have considerable grazing impact on natural bacterial populations.

**Heterotrophic dinoflagellates**

Jeong et al. (2006) and Yoo et al. (2013) reported that the abundance of the heterotrophic dinoflagellate *Pfiesteria piscicida* and morphologically similar heterotrophic dinoflagellates (so called *Pfiesteria*-like dinoflagellates) exceeded 10,000 cells mL⁻¹ (i.e., >1,000 ng C mL⁻¹) and caused red tides in Korean waters. *P. piscicida* isolated from Korean waters is known to feed on bacteria (Jeong et al. 2008). The heterotrophic dinoflagellates *Oxyrrhis marina* and *Gyrodinium* spp., isolated from Korean waters, were also able to feed on bacteria (Jeong et al. 2008). Jeong et al. (2008) further reported that the maximum bacterial ingestion rates of heterotrophic dinoflagellates were 71.3 cells dinoflagellate⁻¹ h⁻¹ for *O. marina*, 23.2 cells dinoflagellate⁻¹ h⁻¹ for *G. cf. guttula*, and 13.7 cells dinoflagellate⁻¹ h⁻¹ for *P. piscicida*. These rates are comparable with those for mixotrophic dinoflagellate (1.2-20.6 cells alga⁻¹ h⁻¹), raphidophytes (11.7-24.5 cells alga⁻¹ h⁻¹), HNFs (4-10 cells alga⁻¹ h⁻¹) (Eccleston-Parry and Leadbeater 1994, Zubkov and Sleigh 1995), and ciliates (150-380 cells ciliate⁻¹ h⁻¹) (Alonso et al. 2000). Therefore, some heterotrophic dinoflagellates may be important predators on marine bacteria (Jeong et al. 2008).

**RECIPROCAL PREDATION BETWEEN BACTERIA AND RED TIDE ORGANISMS**

The pathogenic bacterium *Vibrio parahaemolyticus* is known to be a killer of dinoflagellates, and also to act as prey for red tide dinoflagellates (Seong and Jeong 2011). At *V. parahaemolyticus* concentrations of >1.5 × 10⁶ cells mL⁻¹, *C. polykrikoides* is a victim. At *V. parahaemolyticus* concentration of 1.4 × 10⁵ cells mL⁻¹, *G. impudicum* is also a victim. At *V. parahaemolyticus* concentrations of <1.5 × 10⁶ cells mL⁻¹, *A. carterae, P. minimum*, and *P. micans* are mainly grazers on *V. parahaemolyticus*, whereas at the higher *V. parahaemolyticus* concentration, they may also be victims (Fig. 3). According to these data, Seong and Jeong (2011) proposed that the roles of red tide dinoflagellates and bacteria are reversible, depending on the bacterial concentration. *P. micans* is able to acquire 9.2% of its daily body carbon intake (91.8 pg) from *V. parahaemolyticus*. Thus, *V. parahaemolyticus* may stimulate or partially support the growth of *P. micans*.

On the basis of data derived from studies of bacte-
Taken together, the results of previous studies on the interactions between heterotrophic bacteria and red tide organisms indicate the following roles of each marine component in the dynamics of the other: 1) bacteria can be killers of red tide organisms; 2) bacteria can clear the body of senescent red tide organisms, by accelerating the decline of a red tide and decomposing the red tide organisms; 3) during some red tides, dominant red tide organisms may be the most effective predators of marine bacteria among protistan predators; and 4) bacteria may be too small to be ingested by filter-feeding copepods, whereas many red tide organisms are ingested by the copepods. Red tide organisms may therefore represent a link between bacteria and some zooplankters, which are unable directly to ingest bacteria.

Thus, bacteria may play diverse roles in red tide dynamics, and may even be critical factors affecting the abundance of red tide organisms in Korean waters.

CONCLUSION

Marine heterotrophic bacteria and red tide organisms can act as predators and / or prey in Korean waters. Furthermore, their roles are reversible at any time. Thus, these 2 components may co-exist by cycling materials between each other in marine ecosystems. Several methods for controlling red tides using mass-cultured algicidal bacteria have been developed. However, to evaluate the efficiency of these methods in natural environments, intensive field testing is required.

ACKNOWLEDGEMENTS

We thank Dr. Yeong Du Yoo and Nam Seon Kang for technical supports. This work was supported by the National Research Foundation of Korea Grant funded by the Korea Government/MSICTFP (NRF-C1A-BA001-2010-0020702), Mid-career Researcher Program (2012-R1A2A2A01-010987), Ecological Disturbance Program of KIMST, Long-term change of structure and function in marine ecosystems of Korea program of KIMST/ MOF award to HJJ.

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