

Bacteriocidal effects of brevetoxin on natural microbial communities



Rachel E. Sipler^{a,c,*}, Lora R. McGuinness^a, Gary J. Kirkpatrick^b, Lee J. Kerkhof^a, Oscar M. Schofield^a

^a Rutgers, The State University of New Jersey, Institute of Marine and Coastal Sciences, 71 Dudley Road, New Brunswick, NJ 08901, USA

^b Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA

^c Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, VA 23062, USA

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ABSTRACT

The sensitivity of bacteria to the marine neurotoxins, brevetoxins, produced by the dinoflagellate *Karenia brevis* and raphidophytes *Chattonella* spp. remains an open question. We investigated the bacteriocidal effects of brevetoxin (PbTx-2) on the abundance and community composition of natural microbial communities by adding it to microbes from three coastal marine locations that have varying degrees of historical brevetoxin exposure: (1) Great Bay, New Jersey, (2) Rehoboth Bay, Delaware and (3) Sarasota Bay, Florida. The populations with limited or no documented exposure were more susceptible to the effects of PbTx-2 than the Gulf of Mexico populations which are frequently exposed to brevetoxins. The community with no prior documented exposure to brevetoxins showed significant ($p = 0.03$) changes in bacterial abundance occurring with additions greater than $2.5 \mu\text{g PbTx-2 L}^{-1}$. Brevetoxin concentrations during *K. brevis* blooms range from ~ 2.5 to nearly $100 \mu\text{g L}^{-1}$ with typical concentrations of ~ 10 – $30 \mu\text{g L}^{-1}$. In contrast to the unexposed populations, there was no significant decrease in bacterial cell number for the microbial community that was frequently exposed to brevetoxins, which implies variable sensitivity in natural communities. The diversity in the bacterial communities that were sensitive to PbTx-2 declined upon exposure. This suggests that the PbTx-2 was selecting for or against specific species. Mortality was much higher in the $200 \mu\text{g PbTx-2 L}^{-1}$ treatment after 48 h and $>37\%$ of the species disappeared in the bacterial communities with no documented exposure. These results suggest that toxic red tides may play a role in structuring bacterial communities.

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1. Introduction

Brevetoxins are potent neurotoxins naturally produced by the dinoflagellate *Karenia brevis* (formerly known as *Gymnodinium breve* and *Ptychodiscus brevis*) and several species of the raphidophyte *Chattonella* (reviewed in Landsberg, 2002; Brand et al., 2012; Imai and Yamaguchi, 2012). Blooms of these species and their toxins have been linked to fish, shellfish, marine mammal, marine invertebrate and sea bird mortalities, as well as negative human health effects including neurotoxic shellfish poisoning (NSP) and respiratory distress (Kirkpatrick et al., 2004; Landsberg et al., 2009; Fleming et al., 2011). Chemically,

brevetoxins are a suite of hydrophobic, polycyclic ether compounds (Baden, 1989; Nicolaou et al., 1998; Vilotijevic and Jamison, 2007). There are 2 structural types and at least 9 natural forms of brevetoxin with brevetoxin 2 (PbTx-2) being the most abundant in nature (Baden, 1989; Pierce et al., 2008; Brand et al., 2012). These compounds are known to negatively affect organisms by activating sodium channels leading to depolarization and alteration of the cell membrane (Baden, 1983; Purkerson et al., 1999; Kirkpatrick et al., 2004). Brevetoxins have also been shown to affect cellular calcium channels and likely impact other yet unidentified metabolic enzymes (Drauid et al., 2004; Kitchen, 2010). No matter what the pathway, the series of reactions that occur to a cell during brevetoxin exposure are complex and have been observed even at the gene expression level (Murrell and Gibson, 2011). The end result of brevetoxin exposure is inflammation of the cell and cell death (Purkerson et al., 1999; Murrell and Gibson, 2011).

Toxic *K. brevis* blooms frequently disrupt the marine communities along the West Florida shelf and occasionally along the South Atlantic Bight with a range between Jacksonville, FL and Beaufort,

* Corresponding author at: Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, VA 23062, USA. Tel.: +1 804 684 7486; fax: +1 804 684 7786.

E-mail addresses: sipler@vims.edu (R.E. Sipler), mcguinne@marine.rutgers.edu (L.R. McGuinness), gkikpat@mote.org (G.J. Kirkpatrick), kerkhof@marine.rutgers.edu (L.J. Kerkhof), oscar@marine.rutgers.edu (O.M. Schofield).

NC (Buck and Pierce, 1989; Geesey and Tester, 1993; Tester and Steidinger, 1997). In 2000, brevetoxin production associated with a *Chattonella cf. verruculosa sensu* bloom appeared in Rehoboth Bay, DE and its tributaries (Bourdelaïs et al., 2002). These brevetoxin producing species exist in very different aquatic niches. *K. brevis* blooms nearly annually in the tropical and subtropical oligotrophic waters of the Gulf of Mexico, while *C. cf. verruculosa*, like many *Chattonella* spp. (Imai and Yamaguchi, 2012), is often observed in inland waters including shallow eutrophic canals and bays. This wide geographic range suggests that brevetoxin may impact a large number of diverse estuarine and coastal ecosystems. While extensive research has been done on the effects of brevetoxins on species ranging from zooplankton, marine mammals, humans (Landsberg, 2002; Fleming et al., 2011; Brand et al., 2012), and co-occurring phytoplankton (Kubaneck et al., 2005; Prince et al., 2008, 2010), no studies have been conducted on the direct effect of brevetoxins on bacteria or bacterial community composition.

The relationship between bacteria and phytoplankton, especially many harmful algal bloom species, is complex including known symbiotic, antagonistic, predatory and competitive associations (Cole, 1982; Doucette, 1995; Kodama et al., 2006). Still, the role that many marine toxins, including brevetoxins, play in modulating microbial community structure remains enigmatic. Although algicidal bacteria active against *K. brevis* have been identified in culture (Doucette et al., 1999; Mayali and Doucette, 2002; Roth et al., 2008), it is not understood how these relationships translate to natural microbial assemblages. Some algicidal species even enhance brevetoxin release (Roth et al., 2007). Field observations have thus far provided contrasting evidence of the relationship between bacteria and the toxic species *K. brevis*. There is evidence that bacterial biomass as non-algal particles decrease with increasing *K. brevis* biomass, indicating that *K. brevis* may negatively affect natural bacterial populations (Cannizzaro, 2004; Schofield et al., 2006). Thus it has been suggested that decreased bacterial abundance during *K. brevis* blooms may be linked to brevetoxin production (Schofield et al., 2006). However, there are also examples of increased bacterial abundance and productivity within *K. brevis* blooms compared to surrounding waters (Evans, 1973; Heil et al., 2004; Jones et al., 2010) and yet other studies suggest that there is no relationship between bacteria and *K. brevis* abundances (Buck and Pierce, 1989). These results imply a variable response between bulk bacteria communities and the presence of *K. brevis*.

Like *K. brevis*, much of the research on the relationship between bacteria and *Chattonella* spp. has focused on identifying algicidal bacteria (e.g. Lovejoy et al., 1998; Furuki and Kobayashi, 1991; Liu et al., 2008a). There are also studies that have explored bloom promoting bacteria (Liu et al., 2008b). Although great advancements have been made in these areas, the role that the toxins produced by *Chattonella* spp., specifically brevetoxins, play in structuring the microbial community is relatively unexplored.

Field observations of saxitoxin, produced by *Alexandrium* spp. blooms, show shifts in bacterial species dominance when toxin levels are high (Pomati et al., 2003; Jasti et al., 2005), indicating that some species may be more or less tolerant to saxitoxin than others. Additionally, it is a commonly held belief among those who culture *K. brevis* that axenic growth is rarely, if ever, achieved. So there are likely some bacteria that are critical to the ecology of *K. brevis*, the role of the associated bacteria, and the mechanisms that control competition in the marine environment.

Under nutrient depleted conditions some harmful algal species are more likely to produce allelopathic chemicals/toxins than in nutrient replete conditions (Granéli, 2006). It has been hypothesized that this strategy aids in the reduction of nutrient stress by not only eliminating competitors for limiting nutrients but also gaining nutrients provided by their remineralization (Granéli,

2006). Bacterial cell lysis would provide a significant source of dissolved organic matter (DOM; Middelboe and Lyck, 2002; Kawasaki and Benner, 2006) in low nutrient systems. It is possible that toxins play a role in altering the microbial community composition thereby controlling competition and nutrient regulation in addition to deterring grazing (Granéli and Turner, 2006; Granéli, 2006). The ability to take full advantage of a variety of nutrient resources may give *K. brevis* a competitive edge over other bloom forming phytoplankton (Liu et al., 2001; Bronk et al., 2004; Sipler et al., 2013).

This study investigated the effects of PbTx-2 on the bacterial abundance and community composition of natural bacterial populations from 3 geographically separated regions (NJ, DE, and FL). The range of exposures spanned from no documented exposure (NJ) to rare occurrences (DE) to frequent reports of brevetoxin exposure (FL). The goal of this study was to determine if PbTx-2 negatively impacts natural microbial communities and if geographically separated communities respond similarly to brevetoxins.

2. Methods

Brevetoxin (PbTx-2) was added to three different coastal microbial populations to investigate its affect on the bacterial community abundance and composition. Locations were chosen based on available data of brevetoxin exposure. The three locations, Great Bay, NJ (39°32'22"N, 74°23'13"W), Rehoboth Bay, DE (38°39'45"N, 75°07'53"W) and Sarasota Bay, FL (27°19'54"N, 82°34'34"W), represent communities ranging from no documented exposure to brevetoxins, to occasional (Bourdelaïs et al., 2002) and frequent exposures to bevetoxins (Fire et al., 2007; Pierce and Henry, 2008; Gannon et al., 2009) respectively (Fig. 1). While a lack of documented brevetoxin presence does not necessarily indicate that it has never occurred in these northern areas, the lack of fish kills attributed to brevetoxins, and the lack of high density blooms of brevetoxin producing species does indicate that if present the abundances/brevetoxin concentrations have not been high enough and frequent enough to warrant observation in these highly populated areas. The bacterial community composition samples collected from each of the three sites were compared to the bacterial communities associated with *K. brevis* cultures and a natural *K. brevis* bloom.

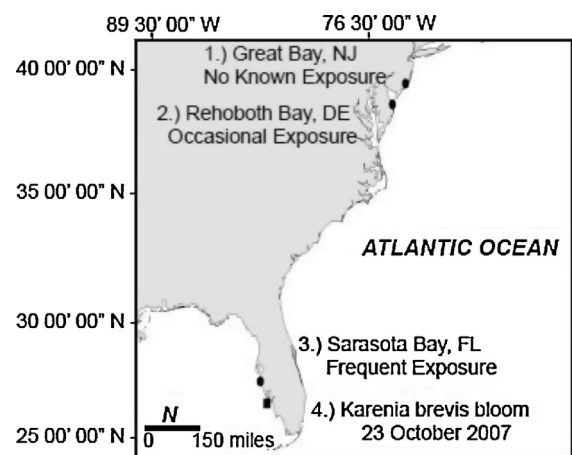


Fig. 1. Map of sample sites. Site 1 is Great Bay, NJ (NJ); site 2 is Rehoboth Bay, DE (DE); site 3 is Sarasota Bay, FL (FL); site 4 is the location of the October 2007 *Karenia brevis* bloom.

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