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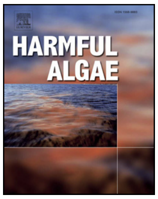

Habitat complexity affects benthic harmful dinoflagellate assemblages in the fringing reef of Rawa Island, Malaysia

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ABSTRACT

Few studies have investigated the effect of fine-scale habitat differences on the dynamics of benthic harmful dinoflagellate assemblages. To determine how these microhabitat differences affect the distribution and abundance of the major benthic harmful dinoflagellate genera in a tropical coral reef ecosystem, a field study was undertaken between April–September 2015 and January 2016 on the shallow reef flat of the fringing reef of Rawa Island, Terengganu, Malaysia. Sampling of benthic dinoflagellates was carried out using an artificial substrate sampling method (fiberglass screens). Benthic microhabitats surrounding the sampling screens were characterized simultaneously from photographs of a 0.25-m^2 quadrat based on categories of bottom substrate types. Five taxonomic groups of benthic dinoflagellates, *Ostreopsis*, *Gambierdiscus*, *Prorocentrum*, *Amphidinium*, and *Coolia* were identified, and cells were enumerated using a light microscope. The results showed *Gambierdiscus* was less abundant than other genera throughout the study period, with maximum abundance of 1.2×10^3 cells 100 cm^{-2}. While most taxa were present on reefs with high coral cover, higher cell abundances were observed in reefs with high turf algal cover and coral rubble, with the exception of *Ostreopsis*, where the abundance reached a maximum of 3.4×10^4 cells 100 cm^{-2} in habitats with high coral cover. Microhabitat heterogeneity was identified as a key factor governing the benthic harmful dinoflagellate assemblages and may account for much of the observed variability in dominant taxa. This finding has significant implications for the role of variability in the benthic harmful algal bloom (BHAB) outbreaks and the potential in identifying BHAB-related toxin transfer pathways and the key vectors in the food webs.

1. Introduction

Many benthic dinoflagellates species are of interest because some produce biotoxins that cause significant human illnesses. Species of *Gambierdiscus*, for example, produce ciguatoxins (e.g., Yasumoto et al., 1977, 1979; Shimizu et al., 1982; Chinain et al., 1999; Litaker et al., 2017), causing ciguatera fish poisoning (CFP) (Yasumoto et al., 1980; Gatti et al., 2015; Chinain et al., 2016; reviewed in Berdalet et al., 2017); outbreaks of *Ostreopsis* cf. *ovata* produce air-borne palytoxin-like analogues that cause respiratory illness and skin irritation to the beachgoers, negatively affecting beach tourism (Ciminiello et al., 2006, 2008, 2010; Tubaro et al., 2011). Other species in the genera *Prorocentrum*, *Amphidinium* and *Coolia* produce various bioactive compounds (e.g., okadaic acid, Yasumoto et al., 1984; amphidinolide, Kobayashi et al., 1986, 1988; cooliatoxin, Holmes et al., 1995; Wakeman et al., 2015). Some of these compounds are responsible for diarrhetic shellfish poisoning (Yasumoto et al., 1984), palytoxin seafood poisoning (Durando et al., 2007) and clupeotoxicity (Onuma et al., 1999). The diverse array of toxins produced by these organisms and their adverse human health effects have led to a broad commitment to increase studies on benthic harmful microalgae worldwide (reviewed in Berdalet et al., 2017).

Surprisingly, one of the most striking unstudied aspects of the biology of benthic dinoflagellates is how small-scale difference in substrates affects the distribution and abundance of these species, and by inference the local risk of toxicity. Given the cells' intimate association

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with the benthos, it has long been noted that, in general, substrate type appears to play a major role in governing the uneven distribution of these organisms (Tindall and Morton, 1998). Few studies, however, have quantitatively categorized the substrate type in a detailed manner that would provide a greater understating on how fine-scale differences in habitat affects benthic dinoflagellate abundance and distribution. To address this issue, we examined the relationship between microhabitat type and the distribution of the major benthic harmful dinoflagellate genera in a fringing reef of Rawa Island, Terengganu, Malaysia.

There is general agreement that structural complexity of coral reef ecosystems creates complex microhabitat types that have noticeable influence on the diversity, composition, and abundance of reef inhabitants, including the benthic dinoflagellates (Graham and Nash, 2013; Teichberg et al., 2018). The specific genera surveyed in this study included *Gambierdiscus*, *Ostreopsis*, *Prorocentrum*, *Amphidinium,* and *Coolia*. Species belonging to these genera often co-occur in the reef ecosystems, although the relative abundances of each genus vary significantly (Yasumoto et al., 1980; Tindall and Morton, 1998; Tosteson et al., 1998; Vila et al., 2001; Tester et al., 2014). Species in these genera can be epiphytic, metaphytic (forming a mucilaginous matrix loosely attached to the substratum) or exist as periphyton within or on the surfaces of sandy sediments. It is believed that dominant genera in the assemblages appear largely dependent on different biotic and abiotic bottom substratum and the degree of turbulent dispersion (Tindall and Morton, 1998). While many studies on the habitat preferences of benthic harmful dinoflagellates have been contradictory (e.g., Okolodkov et al., 2007; Rahman Shah et al., 2013; Rains and Parsons, 2015), Tindall and Morton (1998) elucidated the effects of structural complexity of coral reefs on benthic harmful dinoflagellate communities (System I and II, cf. Tindall and Morton, 1998) in relation to the environmental driving factors controlling the distribution of theses benthic dinoflagellates. Likewise, several studies have associated the increasing abundance of benthic harmful dinoflagellates with increasing macroalgal and/or turf algal covers (Vila et al., 2001; Parsons and Preskitt, 2007; Rongo and van Woesik, 2013; Skinner et al., 2013). In fact, reef disturbance (human exploitation, coastal development, pollution, overfishing) that cause a phase shift from coral to algal-dominated reef communities can provide potential bottom substrates for benthic harmful dinoflagellates to proliferate (Bagnis et al., 1988; Bagnis, 1994; Chinain et al., 1999). Indeed, some studies suggest that CFP epidemics often follow large-scale natural reef disturbances (Turguet et al., 2001; Chateau-Degat et al., 2005; Rongo and van Woesik, 2011, 2013; Chinain et al., 2016). Consequently, the altered composition and abundance of benthic harmful dinoflagellates contributed to increased risk of CFP (Yasumoto et al., 1980; Chinain et al., 2016).

The nature of non-planktic behaviour and patchy distribution of benthic dinoflagellates has greatly complicated the implementation of quantitative sampling strategies (Giussani et al., 2017; Jauzein et al., 2018). This has resulted in various sampling methods in the ecological studies of benthic harmful dinoflagellates that hindered data integration for comparative studies (GEOHAB, 2012) especially for studies focused on reef ecosystems with high structural complexity (Berdalet et al., 2017). Among a variety of sampling strategies, natural substrate collection (macrophytes, sand, rubble) has been the most common methodology adopted. This method, however, demonstrated weak correlations among various macrophytes sampled (e.g., Parsons et al., 2017). The need to implement a standardized sampling strategy for benthic harmful dinoflagellates in a management perspective has been recognized (GEOHAB, 2012), and several sampling protocols have been introduced (Tester et al., 2014; Jauzein et al., 2016, 2018; Mangialajo et al., 2017). The artificial substrate method using fiberglass screens (Kibler et al., 2010; Tester et al., 2014; Jauzein et al., 2016, 2018), provides an alternative approach for the study of community composition of benthic harmful dinoflagellate assemblages regardless of the bottom landscape heterogeneity and structural complexity. While numerous advantages of artificial substrates have been recognized (Tester et al., 2014; Jauzein et al., 2016; Tester and Kibler, 2018), Jauzein et al. (2018) highlighted the utility of this method to normalize spatial and temporal heterogeneity inherent in macrophyte composition and distribution.

While it is understood that reef microhabitats play an important role in structuring benthic dinoflagellate communities, there are few, if any efforts that provide statistically robust studies with well-defined habitat characterization (Tindall and Morton, 1998; Richlen and Lobel, 2011). This study objectively characterized benthic microhabitats on the basis of substrate type and documented how those microhabitat types affect the composition of the associated benthic harmful dinoflagellate communities. Knowing this information has important implications for understanding which microhabitats foster the growth of species responsible for producing toxins that vector in the food web. While coral reef fishes are primarily the main vectors of CFP in humans, other non-fish vectors such as giant clams (Roué et al., 2016), sea urchin (Darius et al., 2018a) and gastropods (Darius et al., 2018b) have been implicated. Too, the potential role of mesograzers in toxins transfer presents a great challenge in understanding the source and sink of biotoxins in the marine food webs (Lewis et al., 1994; Cruz-Rivera and Villareal, 2006). In this study, five dominant, benthic dinoflagellate genera (*Gambierdiscus*, *Ostreopsis*, *Amphidinium, Coolia,* and *Prorocentrum*), each containing toxic species were examined. Multivariate analyses were employed to examine differences among microhabitats and help explain the variability in benthic harmful dinoflagellate taxa composition and abundance.

2. Materials and methods

2.1. Study site description

This study was conducted at Rawa Island, Terengganu (5°57′44.45″ N, 102°40′53.26″S), on the east coast of Peninsular Malaysia (Fig. 1). Sampling was undertaken at the western side of the island, covering a shallow reef flat of about 100 m × 180 m (~20,000 m^2) with a depth of ~3 m. A total of 106 artificial substrate (screen) sampling devices were deployed and collected 24 h later between April 2015 and September 2015. Additional sampling was conducted in January 2016 (Supplementary Table S1). Heavy rainfall and rough sea condition during the wet monsoon season prohibited sampling activities from October to December 2015.

Seawater salinity was recorded using an HI 96822 refractometer (HANNA Instrument Incorporation, USA). Water depth was measured with a portable depth sounder (Speedtech Instruments, USA). HOBO Pendant Temperature/Light data loggers were deployed at sampling sites to record water temperature (°C) and light intensity (μmol photon m^{-2} s^{-1}).

2.2. Sample collection and processing

The artificial substrate method was used in this study (Kibler et al., 2010; Tester et al., 2014). Fiberglass screens were cut into standardized pieces of 10.2 cm^2 × 15.2 cm^2 in size. Each screen was connected to a small sub-surface buoy and a weight (< 200 g) with a monofilament fishing line. The screens were placed 20 cm above the seafloor. In the field, the screens were deployed underwater by SCUBA (Supplementary Fig. S1). A total of nine sampling trips were made throughout the study period. Screens were deployed over various bottom substrates that were characterized simultaneously by photographing a 0.25-m^2 quadrat at each sampling location (see Section 2.3). GPS coordinates of the sites are included in Supplementary Table S1. After 24 h the screen samples were gently retrieved and placed in individual one-litre wide mouth plastic bottles filled with ambient seawater. Samples were then transported to the laboratory for processing after each sampling effort.

Each screen was shaken vigorously for 5–10 s to dislodge attached