



Bacterioplankton assembly and interspecies interaction indicating increasing coastal eutrophication



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HIGHLIGHTS

- Increasing coastal eutrophication linearly increases the importance of deterministic processes that constrained BCCs.
- The buffer capacity of BCCs is limited, with disrupted interspecies interaction occurring under heavy eutrophication.
- The dynamics of bio-indicators closely linked with eutrophication levels and are concordant with their ecological functions.

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ABSTRACT

Anthropogenic perturbations impose negative effects on coastal ecosystems, such as increasing levels of eutrophication. Given the biogeochemical significance of microorganisms, understanding the processes and mechanisms underlying their spatial distribution under changing environmental conditions is critical. To address this question, we examined how coastal bacterioplankton communities respond to increasing eutrophication levels created by anthropogenic perturbations. The results showed that the magnitude of changes in the bacterioplankton community compositions (BCCs) and the importance of deterministic processes that constrained bacterial assembly were closely associated with eutrophication levels. Moreover, increasing eutrophication significantly ($P < 0.001$) attenuated the distance decay rate, with a random spatial distribution of BCCs in the undisturbed location. In contrast, the complexity of interspecies interaction was enhanced under moderate eutrophication levels but declined under heavy eutrophication. Changes in the relative abundances of 27 bacterial families were significantly correlated with eutrophication levels. Notably, the pattern of enrichment or decrease for a given bacterial family was consistent with its known ecological functions. Our findings demonstrate that the magnitude of changes in BCCs and underlying determinism are dependent on eutrophication levels. However, the buffer capacity of bacterioplankton community is limited, with disrupted interspecies interaction occurring under heavy eutrophication. As such, bacterial assemblages are sensitive to changes in environmental conditions and could thus potentially serve as bio-indicators for increasing eutrophication.

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1. Introduction

Patterns of anthropogenic coastal use have undergone considerable changes in recent times, with the advent and expansion of coastal aquaculture, urban, agricultural, and industrial runoff (Fodelianakis et al., 2014; Xiong et al., 2015). As a result, coastal

ecosystems are being threatened by increasing eutrophication (SOA, 2015). Currently, multivariate index has been widely applied to classify water quality. (Primpas et al., 2010; Hou et al., 2016). However, this index does not take into consideration additive, synergistic and antagonistic effects of biota and abiotic factors (Borruso et al., 2015). Microbial communities are generally the first responders to environmental perturbation and can either augment or buffer environmental changes (Labbate et al., 2016). Thus, the application of bacterial bio-indicator could systematically reflect and record both biotic and abiotic (including unmeasured and

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unobserved factors) pressures, even after the contaminants themselves have been fully degraded (Smith et al., 2015). Indeed, natural bacterial communities have been widely applied as in situ environmental indicators that respond to and capture anthropogenic perturbations (Fodelianakis et al., 2014; Xiong et al., 2014; Borruso et al., 2015). Nevertheless, no consensus has been emerged regarding the microbial resistance and resilience to a changing environment (Allison and Martiny, 2008; Shade et al., 2012). For example, consistent associations of specific bacterioplankton groups with nutrient enrichment are detected across different habitats (Fodelianakis et al., 2014), and seasons (Xiong et al., 2015). In contrast, it was reported that microbial community resists perturbation by nutrient enrichment (Bowen et al., 2011). This apparent discrepancy could be due to the sensitivity of microbial communities depending on the eutrophication level (Van Der Gast et al., 2008; Shade et al., 2012). Consistently, both field surveys and laboratory experiments have shown that the magnitude of changes in microbial communities is dependent on pollution levels (Ager et al., 2010; Xiong et al., 2014). However, it is unknown whether this pattern would be disrupted under severe disturbance despite such information being crucial for evaluating the buffer capacity of an ecosystem to increasing anthropogenic perturbations. Recently, it has been proposed that the response of microbial communities to environmental changes is structured by a complex combination of adaptation (e.g., resistance and resilience), replacement (e.g., immigrants dispersed from nearby localities), and interspecies interaction mechanisms (Shade et al., 2012; Xiong et al., 2015; Deng et al., 2016). For these reasons, a better understanding of the ecological processes affecting microbial communities is vital for predicting the responses of ecosystems to a changing environment.

Recently, the distance-decay relationship (DDR) has been applied to quantify the relative robustness of community response to organic pollution (Liang et al., 2015). The slope of the linear regression between logarithmic β -similarities and logarithmic geographic distances reflects the distance decay rate (Nekola and White, 1999), which provides a descriptive statistic for the change rate and therefore can be used to track the stability of a microbial community (Shade et al., 2012). For example, long-term oil exposure significantly retards the distance decay rate of the microbial functional composition (Liang et al., 2015). Two types of processes (deterministic vs. stochastic) have been proposed to explain the DDR (Nemergut et al., 2013; Zhou et al., 2014). Specifically, the spatial environmental heterogeneity selects and sorts microorganisms by deterministic fitness differences between taxa (Van der Gucht et al., 2007); however, this effect could be overridden by stochastic spatial dispersal (e.g., high dispersal rates at local scales due to hydraulic conductivity) of planktonic microorganisms (Finlay, 2002). It is now recognized that deterministic and stochastic processes jointly shape microbial assembly, although their relative importance is still being actively debated (Stegen et al., 2012; Xiong et al., 2015). For example, it has been proposed that nutrient input increases bacterial compositional stochasticity by enhancing ecological drift and weakening species sorting (Zhou et al., 2014), whereas, in contrast, studies show that the increasing concentrations of industrial wastewater contribute a gradual shift from stochastic to more deterministic-based processes (Van Der Gast et al., 2008). These divergent conclusions raise the question of whether and how the relative importance of deterministic processes was affected by increasing coastal eutrophication.

In a given habitat, diverse microbial assemblages interact with one another to form complicated networks through various types of interactions, such as competition and/or mutualism (Faust and Raes, 2012). As such, interspecies interaction determines the responses of a microbial community to disturbance (Shade et al.,

2012; Dang and Lovell, 2016). While deterministic processes (e.g., disturbance-induced environmental filtering) select taxa that are more closely related to co-occurring relatives than would be expected by chance, thereby revealing niche spaces shared by community members (Stegen et al., 2012; Monier et al., 2015). The strength of links among species changes along environmental gradients such that it is increasingly important to determine the buffer capacity to heavy eutrophication. In addition, it has been reported, albeit limited, that synergistic interspecies interaction is critical in maintaining proper functions (Zhu et al., 2016). The complexity of interspecies interaction (e.g., proportion of positive co-occurrence, network size, average clustering coefficient) may therefore provide unique indices for evaluating the stability of microbial communities (Deng et al., 2012; Shade et al., 2012). Given that interaction analyses in microbial ecology are still in its infancy, it is unclear to what extent that the complexity of interspecies interaction is altered with increasing eutrophication.

Coastal areas of the East China Sea are strongly affected by anthropogenic activities, resulting in a complex mixture of pollutants (SOA, 2015). There is ample evidence that the bacterioplankton community compositions (BCCs) are markedly affected by both organic and inorganic pollutants (Xiong et al., 2015; Pringault et al., 2016). However, using a forward selection, our previous work showed that the BCCs were primarily determined by the nutrient variables, rather than the measured heavy metals (Wang et al., 2015). For this reason, here we only explored how eutrophication affects the assembly of bacterial community. To achieve this, we integrated the DDR model (Nekola and White, 1999), the standardized effect size measure (Stegen et al., 2013), and network inference approaches (Deng et al., 2012) to address the following questions: (i) how eutrophication affect the spatial patterns of bacterioplankton communities? (ii) to what extent is the relative importance of deterministic processes altered by increasing eutrophication? and (iii) what is the relationship between the strength of interspecies interaction and eutrophication levels? In addition, given that a bacterial bio-indicator provides quantitative information on the eutrophication level around it (Borruso et al., 2015), we further screened sensitive taxa for indicating eutrophication level. To this end, Illumina sequencing data for a spatial survey of bacterioplankton communities were collected from our previous work, in which showed that the biogeography of bacterial community was determined by spatially structured environmental gradients (Wang et al., 2015). In contrast, here we explored to what extent that the assembly (e.g., determinism and interspecies interaction) of bacterial community was affected by increasing coastal eutrophication from an ecological perspective. This further work revealed that increasing coastal eutrophication linearly enhanced the importance of deterministic processes that constrained BCCs. However, the buffer capacity of bacterioplankton community was disrupted under heavy eutrophication. In addition, bio-indicators were identified to indicate eutrophication levels.

2. Materials and methods

2.1. Data collection and location descriptions

The sequencing data were obtained from the Sequence Read Archive of DDBJ (<http://www.ddbj.nig.ac.jp>), under the open accession number DRA002865. Briefly, the V4 region of bacterial 16S rDNA gene were amplified and paired-end sequenced on an Illumina MiSeq machine (Wang et al., 2015). Biogeochemical data were downloaded from the supplemental information (Wang et al., 2015). We selected four representative locations consisting of Yushan Reserve, Sanmen Bay, Xiangshan Bay and Hangzhou Bay (Fig. S1). All samples were collected within two weeks in summer

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