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# Large-scale seaweed cultivation diverges water and sediment microbial communities in the coast of Nan'ao Island, South China Sea



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### HIGHLIGHTS

# GRAPHICAL ABSTRACT

Effects of Gracilaria cultivation on microbial communities

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- Large-scale cultivation of seaweed Gracilaria lemaneiformis altered ecological processes in the coastal ecosystem, resulting in increased pH and dissolved oxygen, and decreased nutrients.
- Such environmental changes led to divergent microbial communities in the *G. lemaneiformis* cultivation zone compared to the control zone in both water and sediment environments.
- Seaweed-associated microbial groups such as Arenibacter, Croceitalea, Glaciecola, Leucothrix and Maribacter were enriched in the cultivation zone.
- A conceptual model is proposed to summarize major results in this study and guide future studies on relationships among *G. lemaneiformis*, microbial communities, and their environments in this cultivation ecosystem.

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# ABSTRACT

Seaweed cultivation not only provides economy benefits, but also remediates the environment contaminated by mariculture of animals (e.g., fish, shrimps). However, the response of microbial communities to seaweed cultivation is poorly understood. In this study, we analyzed the diversity, composition, and structure of water and sediment microbial communities at a seaweed, *Gracilaria lemaneiformis*, cultivation zone and a control zone near Nan'ao Island, South China Sea by MiSeq sequencing of 16S rRNA gene amplicons. We found that large-scale cultivation of *G. lemaneiformis* increased dissolved oxygen (DO) and pH but decreased inorganic nutrients, possibly due to nutrient uptake, photosynthesis and other physiological processes of *G. lemaneiformis*. These environmental changes significantly (adonis, P < 0.05) shifted the microbial community composition and structure of both water column and sediment samples in the *G. lemaneiformis* cultivation zone, Conceitalea, *Glaciecola, Leucothrix* and *Maribacter* were enriched at the cultivation zone. In addition, we have proposed a conceptual model to summarize the results in this study and guide future studies on relationships among seaweed processes, microbial

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16S rRNA MiSeq sequencing communities and their environments. Thus, this study not only provides new insights into our understanding the effect of *G. lemaneiformis* cultivation on microbial communities, but also guides future studies on coastal ecosystems.

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# 1. Introduction

As land resources decrease and the human population booms, mariculture has increasingly grown to exploit the sea to meet global food demands. For example, China has promoted large-scale mariculture of fish, shellfish, shrimps and seaweeds since the 1980s (Tseng, 1993). However, the flourishing industry of marine animal culture has caused severe eutrophication and other environmental problems in coastal areas (Cao et al., 2007). To ameliorate the water guality of contaminated zones with mariculture of economical animals (such as fish, shell fish), a large scale cultivation of seaweed, Gracilaria lemaneiformis, was introduced as a bioremediation approach at Nan'ao Island, Guangdong Province in 2000 with a cultivation area reaching approximately 1500 ha in 2014 (Yang et al., 2015). Although the cultivation of seaweed significantly improved water quality (Yang et al., 2015) and the local economy, little is known about the impact of large scale G. lemaneiformis cultivation on water and sediment microbial communities as well as microbial responses to G. lemaneiformis cultivation.

Since microorganisms play important ecological roles in coastal ecosystems through recycling dissolved nutrients, and mediating global biogeochemical flux of carbon (C), nitrogen (N), phosphorus (P), sulfur (S) and iron (Azam et al., 1983; Azam and Malfatti, 2007), it is essential to understand how microbial communities respond to environmental changes such as the perturbations from anthropogenic activities (e.g. fishing, mariculture) (Halpern et al., 2007; Halpern et al., 2008; Nogales et al., 2011), severe weather, and climate change (Giovannoni and Vergin, 2012). Previous studies mainly focused on the dynamics of microbial communities across time and space in natural marine ecosystems (Fuhrman et al., 2015; Ghiglione et al., 2012). The response of microbes to mariculture, especially seaweed cultivation, has not been well studied (Blancheton et al., 2013; Tamminen et al., 2011). G. lemaneiformis has been cultivated in Chinese coastal areas to alleviate eutrophication and balance the effects of mariculture of economical animals (Yang et al., 2006; Zhou et al., 2006) and proved to be an efficient nutrient pump by removing large amounts of N and P to support its growth. Also, biopolymers and carbon-rich nutrients such as polysaccharide and alginate, secreted by G. lemaneiformis, add organic substrates to surface water, which can be utilized by microbes (Egan et al., 2013; Lachnit et al., 2013). The changes of environmental properties due to G. lemaneiformis cultivation, such as decreased inorganic nutrients, increased pH, DO, polysaccharides and seaweed detritus (Yang et al., 2015; Yang et al., 2006) may promote changes in the composition, structure and function of microbial communities in both water column and sediment environments.

Recent reports on the epiphytic and endophytic microbial communities of various seaweeds (green alga, red alga and brown alga) based on varying methods such as scanning electron microscope, restriction fragment length polymorphism (RFLP), catalyzed reporter deposition fluorescence in situ hybridization (CARD-FISH), denaturing gradient gel electrophoresis (DGGE) fingerprinting, and 16S rRNA gene sequencing (Falkowski and De Vargas, 2004; Pennisi, 2006) have revealed that seaweed-associated bacteria are host-specific and temporally-variable (Campbell et al., 2015; Hollants et al., 2013b; Hollants et al., 2011; Lachnit et al., 2009; Lachnit et al., 2011; Mancuso et al., 2016). Also, the taxonomically diverse microbial communities associated with seaweed (Armstrong et al., 2001; Burke et al., 2011a) performed important functions for their hosts (Egan et al., 2013). For example, a bacterial core community, consisting of species associated with Gammaproteobacteria, Bacteroidetes, Alphaproteobacteria and Firmicutes, seemed to exist on the surface of host seaweed and exhibited a distinct seaweed-associated life style (Aires et al., 2013; Bengtsson et al., 2012; Hollants et al., 2013a). Many of host-associated bacteria play important roles in anti-fouling, anti-grazing and anti-settlement and protect seaweed from invasion of other organisms including pathogens, fungi and herbivores (Armstrong et al., 2001; Goecke et al., 2010). In addition, seaweed-associated bacterial communities can produce quorum sensing molecules (Singh et al., 2015; Twigg et al., 2014), bioactive compounds (Singh et al., 2011a) and plant growth regulators (e.g. IAA, Cytokinin) (Maruyama et al., 1990; Yokoya et al., 2013) to guarantee normal morphology (Singh et al., 2011b), and development and growth of their host seaweed (Singh and Reddy, 2014). More importantly, a core set of specific bacterial community members, which may not exhibit phylogenetically similarities among different host seaweeds, seem to exist on the seaweed surface and contain similar functions related to host-associated lifestyles (Burke et al., 2011a; Burke et al., 2011b; Campbell et al., 2015; Hollants et al., 2013a). However, little is known about the response of planktonic and benthonic microbial communities to seaweed cultivation. Therefore, it is important to understand the microbial community diversity, composition, structure and function in G. lemaneiformis cultivation systems and their relationships with environmental changes and ecosystem functioning (Fei, 2004).

In this study, we aimed to understand the impact of seaweed cultivation on water and sediment microbial communities as well as microbial responses to seaweed cultivation, and we hypothesized that (i) changes in environmental properties such as decreased nutrients and increased dissolved oxygen resulting from seaweed cultivation would shift the diversity, composition and structure of water and sediment microbial communities; and (ii) certain microbial groups would be enriched in the seaweed cultivation ecosystem. To test those hypotheses, we sampled surface water, bottom water and sediment samples from a cultivation zone (GZ) and a control zone (CZ) at Nan'ao Island in the South China Sea, and analyzed the microbial community diversity, composition and structure by MiSeq sequencing of 16S rRNA gene amplicons. This study provides useful information for our understanding the impact of seaweed cultivation on microbial communities as well as their feedbacks to ecosystems, which will promote our future studies on microbial communities, seaweed, and their environments in the G. lemaneiformis cultivation system.

## 2. Materials and methods

## 2.1. Site description and sample collection

This study was conducted in April 2014 on the coastal area of Shen'ao Bay, Nan'ao Island, where a large scale cultivation of *G. lemaneiformis* was carried out and marine fish were cultured in cages for decades, and the environment of fish culture zone has been eutrophicated with NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup> (Hong et al., 2010; Yang et al., 2006; Zhou et al., 2006). Three sites each were chosen from a seaweed cultivation zone, GZ (the *G. lemaneiformis* cultivation zone, 117°07′05″E, 23°28′05″N) and a natural sea area, CZ (control zone, 117°05′33″E, 23°29′17″N) for this study (Fig. S1). Surface (0.5 m depth) or bottom water (0.5 m above sediment) was collected at each site in 4.0 L and filtered immediately on a 0.2 µm polycarbonate membrane (EMD Millipore GTPP04700, USA). The filters were then stored in a tank filled with liquid nitrogen for DNA extraction. Surface sediments from an area of 0.2 m × 0.2 m and a depth of 0.1 m were sampled

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