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Oomycetes and fungi: important parasites on marine algae

LI Wei^{1,2}, ZHANG Tianyu², TANG Xuexi^{1*}, WANG Bingyao¹

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Abstract

Considering that the field is largely unexplored and its importance to aquaculture, outline of oomycetes and fungi parasiting on marine algae was provided in this paper, including 15 species of oomycetes, six species of chytrids, 31 Ascomycota species and one species of mitosporic fungi. In natrue, both the oomycetes and chytrids frequently occurred and induced prevalences of disease which could destroy the populations of host plants greatly. However, the parasites in Ascomycota on algae have never occurred as epidemics so far. Some issues relating to the field were discussed such as performing tests to satisfy Koch's postulates, investigations of host specificity, interactions between host and parasite and the potential effects of environmental factors on occurrence of a disease, which are urgent in need of further investigations.

Key words: oomycetes, fungi, parasites, marine algae

1 Introduction

Diseases of algae due to parasite infection are quite a common phenomenon in the marine habitat, which can significantly affect population of marine algae in nature as well as in mariculture (Das et al., 2006; Raghukumar, 2006; Murray and Peeler, 2005; Hyde et al., 1998; Raghukumar, 1996). Many reports indicate that a variety of algae from Chlorophyta to Rhodophyta are subjected to infectious diseases caused by biotic agents (protozoans, chromista, fungi, bacteria, parasitic algae, nematodes, virus-like particles) (Weinberger, 2007; Ramaiah, 2006; Murray and Peeler, 2005; Andrews, 1976). Diseases cause the largest economic losses in aquaculture and, fungal infection are second only to bacterial diseases in economic importance (Ramaiah, 2006). For example, "red rot disease" of Porphyra caused by Pythium porphyrae has been very severe in Japan, which destroyed millions of tons of the crop in certain areas within 2-3 weeks (Andrews, 1976). In China, occurrence of this disease frequently reach the highest degree both in October and November every year and entirely destroys Porphyra plants in some cultrual areas (Ding and Ma, 2005).

This paper is motivated by the following factors. On global scale, there are a few references on this topic, however, the last 20 years have seen a significant decrease. Especially, studies or surveys on pathogenic fungi from our waters are scanty. Some economic marine algae such as kelps and *Porphyra* are farmed on a large scale along our coastal waters (Fan et al., 2008; Li et al., 2008; Zhang, 2007) and, diseases of aquaculture often occure and gradually become the one of the most difficult problems to be resolved. It is obvious that more information ralated to some important fungal pathogens of concern in both feral and cultured populations of marine algae will have to increase for successfully combating infection diseases and controlling the foul algae leading to the occurrence of red tide by using fit pathogens.

The classification of Kirk et al. (2008) has been followed here and the parasites under the Phyla Oomycota, Chytridiomycota, Ascomycota and Mitosporic fungi will be discussed in this paper. According to the Kirk's classification, the oomycetes falls under the kingdom Chromista and the three other fungi belong to the kingdom Fungi respectively. Therefore, the pathogens infecting marine algae will be divided into the two groups oomycetes and fungi for offering an brief review on the species, host specificity, symptoms and occurrences of diseases. For avoiding the confusion caused by that one pathogen or one host algae maybe has various scientific names, the species names

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¹ College of Marine Life Science, Ocean University of China, Qingdao 266003, China

² College of Plant Protection, Shandong Agricultural University, Taian 271018, China

^{*}Corresponding author, E-mail: liwei01@ouc.edu.cn

used in this paper are taken from the current scientific names on the two internet addresses: http://www. indexfungorum. org/Names/NAMES.ASP and http://www.japan. sp 2000.org/browse_taxa.php respectively.

2 Pathogenic species of oomycetes

2.1 Species of pathogens and their host specificity

Total 15 species have been reported to infect marine algae and a majority of these parasites are obligate pathogens in algae or diatom (Table 1). Host specificity of oomycetes that are parasitic on marine

algae is poorly studied, primarily because an extensive culture collection is necessary to carry out such investigations (West et al., 2006). So it's very difficult accurately to limit the host specificity of these parasites. Scattered information indicates that host specificity of oomycetes to algae are various between different parasites and most of them are restricted to one class of algae, namely, Bacillariophyta, Chlorophyta, Phaeophyta, or Rhodophyta. However, the three pathogens Petersenia lobata, Pontisma lagenidioides and Stirolpidium andreei are the exceptions with broad host ranging from filamentous green algae to brown algae or red algae (Raghukumar, 1996, 1987; Andrews, 1976; Sparrow, 1969, 1960).

Table 1. Pathogenic species of oomycetes on marine algae

Pathogenic oomycetes on algae	Host algae (at the level of genus)	Host algae	Geographic distribution
Ectrogella perforans	Fragilaria, Licmophora, Podocystis,	Bacillariophyta	Europe, USA
H.E. Petersen	$Striatella,\ Synedra,\ Thalassionema$		
Eurychasma dicksonii	$Ectocarpus,\ Feldmannia,\ Punctaria,$	Phaeophyta	Europe, USA, Greenland
E.P. Wright	Pylaiella, Stictyosiphon, Striaria		
$Eury chasmidium\ tume faciens$	Ceramium	Rhodophyta	Europe, USA
(Magnus) Sparrow			
Lagenisma coscinodisci Drebes	Coscinodiscus	Bacillariophyta	Canada, Europe
$Olpidiopsis\ porphyrae\ {\bf Sekimoto},$	Bangia, Porphyra	Rhodophyta	Japan
Yokoo, Y. Kawam. & D. Honda			
Petersenia lobata	$A glaothamnion,\ Callithamnion,\ Ceramium,$	Phaeophyta,	Europe, USA
(H.E. Petersen) Sparrow	$Gymnothamnion,\ Herposiphonia,\ Polysiphonia,$	Rhodophyta	
	$Pylaiella,\ Seirospora,\ Spermothamnion$		
Petersenia palmariae	Palmariae	Rhodophyta	Canada
Van der Meer & Pueschel			
Petersenia pollagaster	Chondrus	Rhodophyta	Canada
(H.E. Petersen) Sparrow			
Pontisma antithamnionis	Antithamnion	Rhodophyta	Canada
(Whittick & South) M.W. Dick			
$Pontisma\ feldmannii$	$Falkenbergia, \ Trailliella$	Rhodophyta	Europe
(Aleem) M.W. Dick			
Pontisma lagenidioides	$Ceramium,\ Chaetomorpha,$	Chlorophyta,	Europe, India, USA
H.E. Petersen	Valoniopsis	Rhodophyta	
Pythium marinum Sparrow	_	Rhodophyta	USA, Denmark
Pythium porphyrae	Porphyra	hodophyta	China, Japan, USA
Takah. {?} & M. Sasaki			
$Sirolpidium\ andreei$	Acrosiphonia, Ceramium,	Chlorophyta,	Arctic, Greenland,
(Lagerh.) M.W. Dick	$Ectocarpus,\ Spongomorpha$	Phaeophyta,	Europe, USA
		Rhodophyta	
$Sirolpidium\ bryopsidis$	$Cladophora,\ Rhizoclonium$	Chlorophyta	India
(de Bruyne) H.E. Petersen			

Notes: -means host algae at the level of genus is unclear.

Host ranges of *Ectrogella perforans* and *Eurychasma dicksonii* span six genera under Bacillariophyta and Phaeophyta respectively (Raghukumar, 1980a, b; Sparrow, 1969, 1960), which suggest that

the two parasites have wide host selection in certain Phylum of host. Infection experiments (Müller et al., 1999) indicate that an isolate of *E. dicksonii* from the brown alga *Pylaiella littoralis* (Linnaeus) Kjellman could attack 45 species covering 39 genera within 12 orders of the Phaeophyceae.

Recently, *Olpidiopsis porphyrae* was found to be a marine endoparasite and laboratory infection experiments with a wild range of green, brown and red algae reveal that the parasite only infects the two genera *Porphyra* and *Bangia* of red algae (Sekimoto et al., 2008).

An oomycete Olpidiopsis sp. isolated from the red alga Bostrychia moritziana (Sonder ex Kützing) J. Agardh shows evident difference in susceptibility to the different Bostrychia strains from various geographical regions (West et al., 2006). Although Stictosiphonia is integrated with Bostrychia in molecular phylogeny (Zuccarello and West, 2006), only one of the species, S. intricata (Bory de Saint-Vincent) P.C. Silva was susceptible, however, both S. kelanensis (Grunow ex E.Post) R.J. King & Puttock and S. tangatensis (Post) R.J. King & Puttock were no-susceptible to the parasite (West et al., 2006). All the brown or green algae tested in infection experiments were non-susceptible to infection (West et al., 2006).

It is notable that host specificity of *Petersenia palmariae* is such strong that this parasite was reported to be specific to *Palmaria mollis* (Setchell & N.L. Gardner) Van der Meer & C.J. Bird and did not attack another red algae *Gracilaria tikvahiae* Mclachlan, *Chondrus crispus* Stackhouse, *Ceramium rubrum* C. Agardh, *Seirospora interrupta* (J.E. Smith) F. Schmitz and even *Palmaria palmata* (Linnaeus) Kuntze (Van der Meer and Peuschel, 1985).

Initially, Pontisma lagenidioides was reported to occur exclusively in the red alga Ceramium sp. as a week parasite or a saprophyte because it thrived best when the alga was under unfavourable conditions (Sparrow, 1960). Further studies show that the species appears to be very host specific as it does infect the green alga Chaetomorpha antennina (Bor de Saint-Vincent) Kützing, but has no infection ability to other green alga like Cladophora, Ulva sp. and even Chaetomorpha linum (O.F. Müller) Kützing (Raghukumar, 1996).

Pythium porphyrae can cause the "red rot disease" of the red alga Porphyra which is commercially cultivated as a major food crop in Japan (Park et al., 2001a, b; Kazama, 1979). In China, Ding and Ma (2005) reported that the pathogen appeared to be the causative agent of the disease of the cultivated P. yezoensis Ueda and P. haitanensis T.J. Chang & B.F. Zheng. Meanwhile P. pulchra G.J. Hollen-

berg, *P. nereocystis* C.L. Anderson and *P. cuneiformis* (Setchell & Hus) V. Krishnamurthy were found to be sensitive to *P. porphyrae* (Kazama, 1979). Considering these mentioned above, it is thought that *P. porphyrae* could attack all species of *Porphyra* if the environmental factors are fit for infection.

2.2 Occurrence and symptoms of disease

The parasites of oomycetes frequently occurred and induced prevalences of a disease in natural or aquacultural populations of host plants. Characteristic symptoms such as changes in colour, rot lesions and abnormal growth may exhibit in infected host marine algae caused by parasitic species of oomycetes.

Ectrogella perforans is one of the devastating obligate parasites of diatoms and was reported to have destroyed about 99 percent population of the diatom Licmophora sp. in one season (Sparrow, 1969). And further studies suggest that the optimum temperature for the parasite infection is 15 °C and infection percentage is higher in light than in dark (Raghukumar, 1996, 1978). With the progress of infection, the diatom infected by E. perforans will show a series of breakdown of host organelles, such as chromatoplasts, mitochondria and nucleus. In the late stage of infection, the sporangium of the parasite occupying the whole cell and often disintegrating structures of the host organelles are seen around the sporangium (Raghukumar, 1980a, b).

The host cell infected with Eurychasma dicksonii will be stimulated to abnormal growth in the early infection stage. But infection by this pathogen frequently may be overlooked because the zoosporangia of the pathogen look much like unilocular sporangia of its host brown alga (Jenneborg, 1977). Laboratory experiments show that the species could infect the two red algae Pylaiella littoralis (L.) Kjellman and Acinetospora crinita (Carmichael) Kornmann from 4 °C to 23 °C that is the lethal limit temperature of host algae (Müller et al., 1999).

Lagenisma coscinodisci was described as an endobiotic parasite of the marine diatom Coscinodiscus centralis Ehrenberg from the North Sea and Western Washington coast (Gotelli, 1971). In Weser estuary of northern Germany, it was reported that about 13 percent infection in natural population of Coscinodiscus was caused by the parasite (Raghukumar, 1996).

Olpidiosis porphyrae is a serious pathogen of the red algae *Porphyra* in China and Japan, which often occurred together with *Pythium porphyrae* in host plants (Sekimoto et al., 2008; Ma et al., 2007; Ding

and Ma, 2005). Originally, the disease caused by this pathogen is called "chytrid blight disease", but Migita (1969) proposed that this disease should be called "Olpidiopsis disease" because the pathogen should be a species of the genus Olpidiopsis and not a chytrid. Sekimoto et al. (2008) resolved the above disputes and described the pathogen as a new species of Olpidiopsis based on the thallus morphology, host specificity and molecular data.

Pontisma lagenidioides has been reported as a potential pathogen of the green alga Chaetomorpha antennina from western and eastern coastal water of the South India penninsula (Raghukumar, 1987). The typical symptom of infection by this parasite is of that the infected cells appear distinctly brownish and spreads from the tip downward of the algal filament (Raghukumar, 1996), because the host chloroplast is changed by infection. Other two marine green algae Cladophora liebetruthii Grunow and Rhizoclonium sp. infected with Sirolpidium bryopsidis showed similar symptoms with C. antennina harboring P. lagenidioides and the infected terminal and subterminal cells are hypertrophied and distinctly brown (Raghukumar, 1986a). Further studies indicate that infection resulted in a sharp decrease in chlorophyll content with concomitant increase in the phaeo-pigments in the diseased plants (Raghukumar and Chandramohan, 1988).

Pythium porphyrae arose the red alga Porphyra suffering from the "red rot disease" that destroyed millions of tons of the crop in certain areas within 2–3 weeks in Japan (Andrews, 1976). In China, the parasite caused great economic losses every year (Ding and Ma, 2005). Beside the above, the disease has been reported to occur on both the Pacific and Atlantic coasts of North America (Kazama, 1979), which suggesting that the parasite is worldwide. Thalli of Porphyra infected by P. porphyrae show rapidly developing somewhat circular lesion of variable sizes and the central region of the lesion is bright green. As in-

fection continuted the colour of circular lesion would change to red and also the algal cells rot (Ding, 2006; Ma, 1996; Kazama, 1979). Arasaki (1947) reported that the pathogen is transmitted via zoospores with relatively warm winter seawater temperatures (24–28 °C), low salinity and plant overcrowding favoring the occurrence and severity of the disease. Considering its devastating effects to Porphyra mariculture, detailed pathological, physiological and ultrastructual studies have been made on this host parasite interactions (Ding and Ma, 2005; Uppalapati et al., 2001; Uppalapati and Fujita, 2000). Park et al. (2001a, b) developed an effective method for quantifying zoospores number in seawater by employing competitive PCR in conjunction with an internal standard DNA and to estimate the amount of P. porphyrae zoospores during the growing season. Their study is very important to be able to quickly assess the amount of zoospores prior to an outbreak of the disease and is favoring to make out disease treatments timely for avioding disease occurrence.

3 Pathogenic species under the Kingdom Fungi

3.1 The Phyla Chytridiomycota infecting marine algae

Thalassochytrium gracilariopsidis was first reported from laboratory cultures of the red alga Gracilariopsis sp. and, the chytrid was considered as an endosymbiotic fungus because it does not appear to cause major harm to its host (Nyvall et al., 1999).

Besides an undetermined species *Coenomyces* sp. infecting the green alga *Cladophora* sp., four species have been reported to be pathogens of marine algae (Table 2).

Chytridium polysiphoniae was often recorded from India coasts as an epibiotic pathogen of both the red alga Centroceras clavulatum (C. Agardh) Montagne

Table 2. Pathogenic species under the Phyla Chytidiomycota infecting marine algae

Pathogenic chytrids on algae	Host algae	Host algae	Geographic
	(at the level of genus)		distribution
Chytridium polysiphoniae E. Cohn	Centroceras, Sphacelaria	Rhodophyta, Phaeophyta	India
$Chytridium\ megastomum\ {\it Sparrow}$	Ceramium	Rhodophyta	USA
Coenomyces sp.	Cladophora	Chlorophyta	India, USA
Olpidium rostriferum Tokun.	$Cladophora,\ Rhizoclonium$	Chlorophyta	India
Rhizophydium littoreum Amon	$Bryopsis,\ Codium$	Chlorophyta	Europe
$Thal assochytrium\ gracilariopsid is$	Gracilariopsis	Rhodophyta	Sweden
Nyvall, M. Pedersén & Longcore ¹⁾			

Notes: 1) May be an endosymbiotic fungus.

and the brown algae Sphacelaria sp. and Pylaiella littoralis (Ramaiah, 2006; Raghukumar, 1986b). Further studies show that the species could attack 23 species covering 19 genera in eight orders of Phaeophyceae (Müller et al., 1999). A severe infection was reported in India and caused disapperance of the brown alga Sphacelaria sp. during January 1989 (Ramaiah, 2006). The fungus shows great obligate parasitic nature and could not be cultured by using pine pollen as baits in seawater nor on killed algae. Healthy algae will become susceptible to infection in the culture condition with salinity of 25 psu and temperature 30 °C in laboratory experiments (Raghukumar, 1986b). Adverse results were provided by Müller et al. (1999), their experiments indicated that the species had a narrow temperature range from 4 to 15 $^{\circ}\mathrm{C}$ and the pathogen will die when temperature reach to 16 °C. These results suggest that the infection biology of the pathogenic chytrid will be virous between different geographic isolates.

Olpidium rostriferum is an endobiotic chytrid parasite that is commonly found in India waters in the green algae Cladophora and Rhizoclonium sp. (Ramaiah, 2006; Chandramohan, 1997). The infected cells become hypertrophied and appear brown in colour (Raghukumar, 1996). The other parasites Coenomyces sp. was found to attack the green alga Cladophora sp., however, no visible morphological changes have been observed (Sparrow, 1960). The salinity of marine environment maybe is one of the important factors affecting the infections of the above two pathogens. Raghukumar (1996) reported that both O. rostriferum and Coenomyces sp. occur in maximum during July to September which is the period of a heavy inflow of fresh water into the coastal marine waters in the areas where infection occurred.

3.2 Pathogens under the Phyla Ascomycota

Not like pathogenic species of oomycetes which can induce prevalences in host populations in nature, the fungal diseases caused by Ascomycota on algae have never occurred as epidemics so far. Kohlmeyer and Kohlmeyer (1979) have made a classic detailed review and listed 31 species parasites from marine algae in the monograph "Marine Mycology: the Higher Fungi". The monograph is recommended to be read by anyone who is interesting with this group of fungal diseases.

Another species *Turgidosculum ulvae* (G.M. Reed) Kohlm. & E. Kohlm. from the green alga

Blidingia minima var. vexata (Setchell & N.L. Gardner) J.N. Norris was reported by Kohlmeyer and Volkmann-Kohlmeyer (2003), however, they pointed that the association between the host alga and *T. ulvae* is mycophycobiosis.

3.3 Mitosporic fungi infecting marine algae

Only one species, Sphaceloma cecidii Kohlm., was reported exclusively in galls caused by species of Haloguignardia in Cystoseira, Halidrys, and Sargassum (Kohlmeyer and Kohlmeyer, 1979; Kohlmeyer, 1971). The fungus can damage the gall tissues by rupturing the outer cell layers and is considered as a hyperparasite because of its restriction to diseased tissues.

4 Summary and discussion

The field of algae-inhabiting marine fungi is largely unexplored and only a few mycologists and phycologists have been involved in such research. Although more than 50 fungal species infecting marine algae have been found at present, our knowledge of them is still scanty and some issues are in urgent need of investigation.

4.1 Performing tests to satisfy Koch's postulates

Koch's postulates have four criteria that are essential to prove the causal organism of any disease in nature: (1) the agent must be present in every case of the disease; (2) the agent must be isolated from the host and grown in a lab dish; (3) the disease must be reproduced when a pure culture of the agent is inoculated into a healthy susceptible host; and (4) the same agent must be recovered again from the experimentally infected host (http://whyfiles.org/012mad_cow/7.html).

Raghukumar (1996) pointed that it is obligatory to establish these postulates with regard to fungal parasites in marine algae also. However, most of species mentioned above have not been performed tests to satisfy Koch's postulates because of that the ability to culture host plants would be a prerequisite and some parasites (most species of oomycetes and chytrids) cannot be cultured in the routine laboratory media (Raghukumar, 1996; Kolhmeyer and Kolhmeyer, 1979). So the cooperation between phycologists and mycologists is necessary.

4.2 Investigations of the host specificity

It is very important to evaluate the potential host

plants being prone to be attacked by a parasites in nature or aquacultural conditions via investigating host specificity of a parasite. Meanwhile, the information on immunological chracteristics and molecular phylogeny of the plants will provide us some elicitations in the evaluation of host specificity of a parasite. Potin et al. (2002) suggested that natural immunity traits of marine algae appear to be phylum- or environment-specific. Recent data indicate that the host plants that have the similar molecular phylogeny tend to be infected by one same pathogen (West et al., 2006). These clues may be the reason why most of fungal parasites were retricted to a certain phylum of host algae.

West et al. (2006) reported that isolates of *Bostrychia moritziana* from Madagascar and South Africa were susceptible to *Olpidiopsis* sp., but those from Mexico, Brazil and Australia were not. Similar studies on geographic diversity of host specificity of a parasite should be encouraged, which is very important to evaluate the spread risk of a disease between countries or locations through international trade or other ways (Murray and Peeler, 2005).

4.3 Interactions between host algae and para sites

To understand the fungl-algal relationships we have to know infection processes of pathogens and possible morphological or physiological changes caused by a disease in host cells. Although there are a few references relating to ultrastructural studies of marine algae and their hosts (Sekimoto et al., 2008; Ding and Ma, 2005; Uppalapati et al., 2001; Uppalapati and Fujita, 2000; Raghukumar and Chandramohan, 1988; Raghukumar, 1987, 1980a, b, 1978; Amon, 1984; Kolhmeyer and Kolhmeyer, 1979; Adrews, 1977; Kazama and Fuller, 1970), there is still little detailed information on most aspects of infection processes, including the mode of host infection (the recognition of host, the settlement and germination of spores, the penetration of the germ or other hyphae into the host cell or tissue) and fungal growth in the host (West et al., 2006; Potin et al., 2002; Correa, 1996; Raghumukar, 1996).

It is not sure whether there are some enzymes participating in the penetration into marine host algae by a pathogen in nature environment, however, some studies show that terrestrial oomycetes and fungi have similar weaponry (degradation of enzymes and mechanical pressure) to attack plants (Latijnhouwers et al., 2003) and many microorganisms associated with apparently healthy macroalgae have the enzymatic capacity to disintegrate tissues of their host (Weinberger, 2007), suggesting that the same mechanism of penetration may exist in between pathogens and their marine algae hosts.

On the other hand, marine plants are not passive participants in biotic interactions, and that they can actively alter their defense strategies when they suffer from various attackers. Some defense strategies on macroalgae suffering from agar degrading bacteria were reviewed (Weinberger, 2007). West et al. (2006) thought that there might be chemical or physical allelopathy responses in cells of red algae that evolved to reject *Olpidiopsis* sp., a fungal pathogen. But there have no reports on what defense reponses of marine algae will be involved when a fungal parasites occur so far. It is undoubtly that to integrate marine plant biology, chemistry and ecology into this area of research will improve our understanding of interactions between host algae and fungal parasites.

4.4 How important are environmental factors affecting the occurrence of a disease

Environmental factors consist of both biotic and unbiotic aspects, which are undoubtful to have important effects on the occurrence of a disease. Muchlstein et al. (1988) reported that some chemical compounds could stimulate chemotactic responses of zoospores of the chytrid *Rhizophydium littoreum*, which was supposed as an adaptation to find host palnts or avoid unfavorable environments. Meanwhile positive phototaxis also exsit in *R. littoreum* (Muchlstein et al., 1987). Aquacultural practices frequently result in high population densities and other stresses (extreme temperature or low oxygen) which increase the risk of infection emergence and spreading (Murray and Peeler, 2005).

Some researchers pointed that although the infectious disease caused by Ascomycota on algae have never occurred as epidemics, the situation may change if algae become predisposed to infection by stress caused, for instance, by thermal and chemical pollution (Correa, 1996; Kolhmeyer and Kolhmeyer, 1979; Andrews, 1976). Meanwhile, unfortunately, it is well known that marine pollution is becoming a concern of all the world and will increase stresses on the growth or reproduction of some marine algae, which will further affect the interactions of pathogens and their hosts. Therefore it is the time that we should pay more at-

tention to the topic.

Polychete worms exist in marine environment commonly. Kohlmeyer (1971) thought that epiphytic animals damage the air vesicles of Sargassum and make the alga susceptible to fungal attack. It is obvious that marine worms play a key role in occurrence of a disease, however, the tri-relationship between algae, fungus and worms have not been studied. Microorganisms grow to higher densities in water than in air, so the aquatic environment generally favors the development of microbes and the formation of biofilms on the surface of marine algae (Weinberger, 2007). Few researches suggested that the biofilms not only have been shown to provide protection from settlement by other micro- or macrofoulers, but also identified as the causative agents of infectious diseases (Weinberger, 2007; Correa and Sanchez, 1996). So the information on the analysis of the epiphytic microorganism communities and their potential effects on a disease need further investigations.

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