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Cryptic diversity within the harmful dinoflagellate *Akashiwo sanguinea* in coastal Chinese waters is related to differentiated ecological niches

Zhaohe Luo[a], Weidong Yang[b], Chui Pin Leaw[c], Vera Pospelova[d], Gwenael Bilien[e], Guat Ru Liow[c], Po Teen Lim[c], Haifeng Gu[a,*]

[a] Third Institute of Oceanography, SOA, Xiamen, 361005, China
[b] College of Life Science and Technology, Jinan University, Guangzhou 510632, China
[c] Bachok Marine Research Station, Institute of Ocean and Earth Sciences, University of Malaya, 16310 Bachok, Kelantan, Malaysia
[d] School of Earth and Ocean Sciences, University of Victoria, OEASB A405, P. O. Box 1700 16 STN CSC, Victoria, British Columbia, V8W 2Y2, Canada
[e] Ifremer, LER BO, Station de Biologie Marine, Place de la Croix, BP40537, F-29185 Concarneau Cedex, France

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ABSTRACT

Blooms of the harmful dinoflagellate *Akashiwo sanguinea* are responsible for the mass mortality of fish and invertebrates in coastal waters. This cosmopolitan species includes several genetically differentiated clades. Four clonal cultures were established by isolating single cells from Xiamen Harbour (the East China Sea) for morphological and genetic analyses. The cultures displayed identical morphology but were genetically different, thus revealing presence of cryptic diversity in the study area. New details of the apical structure complex of *Akashiwo sanguinea* were also found. To investigate whether the observed cryptic diversity was related to environmental differentiation, 634 cells were obtained from seasonal water samples collected from 2008 to 2012. These cells were sequenced by single-cell PCR. For comparison with Chinese material, additional large subunit ribosomal DNA sequences were obtained for three established strains from Malaysian and French waters. To examine potential ecological differentiation of the distinct genotypes, growth responses of the studied strains were tested under laboratory conditions at temperatures of 12 °C to 33 °C. These experiments showed four distinct ribotypes of *A. sanguinea* globally, with the ribotypes A and B co-occuring in Xiamen Harbour. Ribotype A of *A. sanguinea* was present year-round in Xiamen Harbour, but it only bloomed in the winter and spring, thus corresponding to the winter type. In contrast, *A. sanguinea* ribotype B bloomed only in the summer, corresponding to the summer type. This differentiation supports the temperature optimum conditions that were established for these two ribotypes in the laboratory. Ribotype A grew better at lower temperatures compared to ribotype B which preferred higher temperatures. These findings support the idea that various ribotypes of *A. sanguinea* correspond to distinct ecotypes and allopatric speciation occurred in different climatic regions followed by dispersal.

1. Introduction

By definition, cryptic species are morphologically indistinguishable despite being genetically different (Bickford et al., 2007). They are classified as one nominal species but some populations are reproductively isolated. Thus the isolated populations belong to different biological species. Cryptic species have long been recognized (e.g., Montresor et al., 2003), but only recently the speed of discovery has accelerated due to sequencing technology. Cryptic species have been reported in numerous marine organisms, including unicellular protists (e.g., picocyanobacteria (Farrant et al., 2016), prasinophytes (Šlapeta et al., 2006), coccolithophores (Saez et al., 2008), foraminifera (Darling et al., 2000), diatoms (Amato and Montresor, 2008), and dinoflagellates (Montresor et al., 2003)), macroalgae (e.g., red algae (Payo et al., 2013; Muangmai et al., 2016)), and marine animals (e.g., scyphozoans (Dawson and Jacobs, 2001) and rotifers (Suatoni et al., 2006; Montero-Pau et al., 2011).

Marine micro-eukaryotes often have large census population sizes and high dispersal potential. Therefore, they have been considered to have a cosmopolitan distribution, as postulated by the “everything is everywhere” hypothesis (Baas-Becking, 1934; Finlay, 2002). Allopatric speciation, however, does occur in

* Corresponding author.
E-mail address: guhaifeng@tio.org.cn (H. Gu).

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