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ORIGINAL ARTICLE

Reverse transcriptase genes are highly abundant and transcriptionally active in marine plankton assemblages

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Genes encoding reverse transcriptases (RTs) are found in most eukaryotes, often as a component of retrotransposons, as well as in retroviruses and in prokaryotic retroelements. We investigated the abundance, classification and transcriptional status of RTs based on *Tara* Oceans marine metagenomes and metatranscriptomes encompassing a wide organism size range. Our analyses revealed that RTs predominate large-size fraction metagenomes ($>5 \mu$ m), where they reached a maximum of 13.5% of the total gene abundance. Metagenomic RTs were widely distributed across the phylogeny of known RTs, but many belonged to previously uncharacterized clades. Metatranscriptomic RTs showed distinct abundance patterns across samples compared with metagenomic RTs. The relative abundances of viral and bacterial RTs among identified RT sequences were higher in metatranscriptomes than in metagenomes and these sequences were detected in all metatranscriptome size fractions. Overall, these observations suggest an active proliferation of various RT-assisted elements, which could be involved in genome evolution or adaptive processes of plankton assemblage.

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Introduction

Transposable elements (TEs) have been found in virtually all eukaryotes and 80% of prokaryotes sequenced so far (Hua-Van *et al.*, 2011). They are usually considered as selfish DNA with the capacity to proliferate inside the genome (Doolittle and Sapienza, 1980; Orgel and Crick, 1980). Most organisms have no efficient way of eliminating these

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¹¹Current address: Biological and Environmental Sciences and Engineering Division, Center for Desert Agriculture, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia. Received 27 April 2015; revised 27 August 2015; accepted 22 September 2015 potentially deleterious genetic elements from their genomes, although different mechanisms that silence the activity of TEs are being increasingly revealed (Galagan *et al.*, 2003; Slotkin and Martienssen, 2007; Siomi *et al.*, 2011; Watanabe *et al.*, 2013). In spite of their parasitic nature, TEs also provide beneficial effects on the evolution of their hosts (Dunlap *et al.*, 2006; Slotkin and Martienssen, 2007; Casacuberta and Gonzalez, 2013; Gifford *et al.*, 2013; Riordan and Dupuy, 2013; Bennetzen and Wang, 2014). Characterizing the distribution and classification of TEs is thus important to better evaluate their role in shaping the evolution, structure and function of genomes across the whole tree of life.

TEs are traditionally split into two different classes: Class I TEs (retrotransposons) and Class II TEs (DNA transposons), differing in their mode of transposition (Wicker *et al.*, 2007). Retrotransposons

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