



Review

New insight into the RNA aquatic virosphere via viromics

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ARTICLE INFO

Keywords:

RNA virus
Viromics
Metatranscriptomics
Viral ecology
Aquatic microbiology
Picornavirales

ABSTRACT

RNA viruses that infect microbes are now recognized as an active, persistent and important component of the aquatic microbial community. While some information about the diversity and dynamics of the RNA viroplankton has been derived from culture-based and single gene approaches, research based on viromic and metatranscriptomic methods has generated unprecedented insight into this relatively understudied class of microbes. Here, the relevant literature is summarized and discussed, including viromic studies of extracellular aquatic RNA viral assemblages, and transcriptomic studies of active and associated RNA viruses from aquatic environments followed by commentary on the present challenges and future directions of this field of research.

1. Introduction

1.1. The aquatic viroplankton

The most abundant and diverse group of biological entities in aquatic environments are the protists, prokaryotes, and viruses that comprise the microbial community. Microbes play a critical role in the cycling of nutrients and energy, and therefore understanding the dynamics and interactions of this group is vital to understanding the ecology of aquatic ecosystems as a whole. An important, but relatively understudied, component of the microbial community is the viruses.

The study of aquatic viruses that infect microbes has focused almost exclusively on viruses with double stranded (ds) genomes, and for good reason. Viruses with dsDNA genomes are the most abundant (Wigington et al., 2016) and diverse (Suttle, 2016) microbes in aquatic environments. They regulate host abundance and influence population structure, catalyze evolution through the mediation of gene exchange (reviewed in (Suttle, 2007)) and ultimately modify biogeochemical cycles of fundamental importance (reviewed in Weitz and Wilhelm, 2012). Double-stranded DNA phages are undoubtedly major contributors to the viroplankton (community of extracellular aquatic viruses), however, it is now apparent that this assemblage is more diverse than previously appreciated. Communities of largely uncharacterized viruses with single-stranded (ss)DNA (Labonté and Suttle, 2013), and ssRNA and double-stranded (ds)RNA genomes appear to be ubiquitous and widespread in a range of aquatic environments (see below). In fact,

there are limited data that suggest that at times the abundance of RNA viruses can exceed that of dsDNA phages (Steward et al., 2013). However, a comprehensive survey of the morphology of viruses from the world's oceans indicate that this may not be the status quo (Brunet et al., 2013). Moreover sequences closely related to a group of viruses with massive dsDNA genomes have been identified in marine microbial metagenomic libraries (Monier et al., 2008), suggesting that these viruses are also persistent constituents of the virus community. Integrating the diverse and complex groups that comprise the viroplankton into a cohesive ecological picture presents a substantial challenge, and yet it is essential if we are to attain a better understanding of aquatic microbial ecology.

The observation that viruses with a range of genome types exist in aquatic environments raises the question of whether it matters from an ecological perspective, if a virus has a RNA or dsDNA genome. Although the ecological ramifications of a virus's genome composition has yet to be elucidated, the most parsimonious answer would seem to be yes. The activity of a virus is inextricably linked to the nucleic acid composition of its genome. If we summarize the general characteristics of the RNA and dsDNA viruses currently in the ICTV database (<https://talk.ictvonline.org/taxonomy/>), in general, RNA viruses differ from dsDNA viruses in the following ways: the replication of the RNA viral genome is prone to orders of magnitude more error; replication takes place in the cytoplasm; the average genome size is significantly smaller; there are fewer species of RNA viruses that infect prokaryotes; and, with the important exception of retroviruses, RNA viruses do not

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<https://doi.org/10.1016/j.virusres.2017.11.008>

Received 15 August 2017; Received in revised form 7 November 2017; Accepted 7 November 2017

Available online 11 November 2017

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expressly integrate their genome into the chromosome of their host. These fundamental differences between RNA and DNA viruses impact the dynamics of the host-virus interaction and ultimately the overall functioning of the ecosystem.

1.2. Microbial RNA viruses in aquatic habitats: viral isolates

The first data on RNA viruses in the ocean were based on the isolation of RNA viruses that infect aquatic animals of economic importance. These viruses span all possible genome configurations and infect a suite of invertebrates, fish, seabirds and marine mammals (Lang et al., 2009). Although informative and important, these studies did not contribute to an understanding of the ecology of aquatic RNA viruses: that is their abundance, diversity, interactions and role in key energy, nutrient, and evolutionary dynamics.

Early indications that RNA viruses may be important contributors from an ecological perspective resulted from the isolation of viruses that infected various species of phytoplankton i.e. photosynthetic single-celled eukaryotes (protists) that form the base of the aquatic food web. RNA viruses have now been isolated that infect most major taxa of photosynthetic protists. These include diatoms (Kimura and Tomaru, 2015; Nagasaki et al., 2004a; Shirai et al., 2008; Tomaru et al., 2009; Tomaru et al., 2012), dinoflagellates (Nagasaki et al., 2004b) raphidophytes (Tai et al., 2003), prasinophytes (Brussaard et al., 2004) and thraustochytrids (Takao et al., 2006). Surprisingly, there has only been one report of an RNA phage isolated from an aquatic environment (Hidaka and Ichida, 1976). With some exceptions, these viruses are lytic, have small capsids, large burst sizes and have positive-sense, single stranded genomes (Fig. 1).

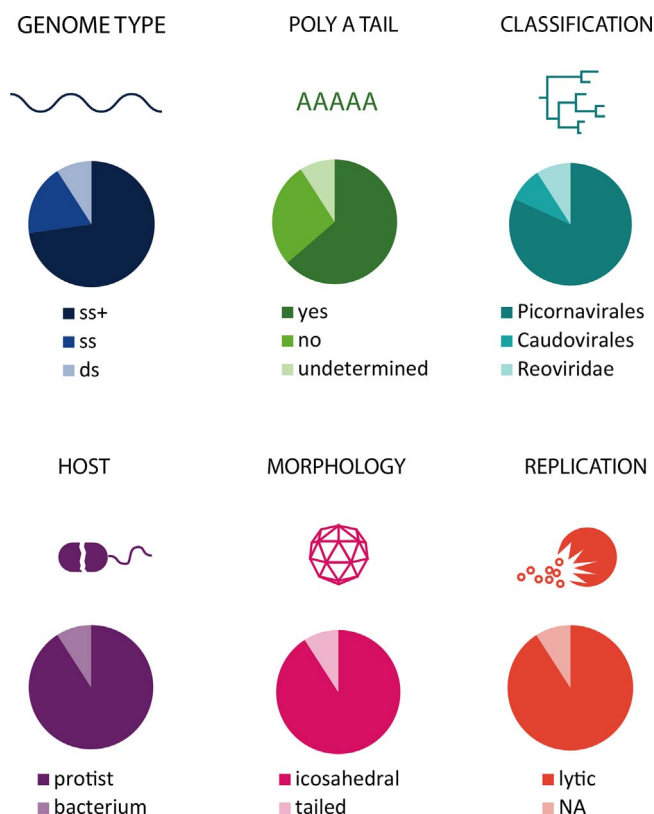


Fig. 1. Portrait of a consensus aquatic RNA virus.

The interpretation of viromic data still is largely dependent on the annotated genomes of viral isolates. This panel of graphs summarizes the most common features of particular relevance to the analysis of viromic data of an aquatic RNA virus based on the characteristics of the 11 published RNA viruses that infect aquatic microbes with sequenced genomes.

1.3. Microbial RNA viruses in aquatic habitats: single-gene surveys

Studies based on cultivation independent approaches indicate that the diversity among the marine RNA viruses far exceeds, and is not well represented by, the limited number of isolates currently in hand. In an early study, an RT-PCR assay for RNA-dependent RNA polymerase (RdRP) genes was used with extracted RNA from seawater to survey the diversity within a “superfamily” of RNA viruses known as the picorna-like viruses (Culley et al., 2003). None of the environmental sequences detected fell within previously established virus families, suggesting that the four clades formed by these sequences may represent four new families of RNA viruses (Culley et al., 2003). A subsequent study was conducted that again assessed the diversity of picorna-like viruses in seawater. This work included the direct filtration of relatively small volumes of water and RT-PCR amplification of a RdRP gene fragment using improved primer sets (Culley and Steward, 2007). Viral polymerase sequences were amplified from several distinct aquatic environments, including an estuarine urban canal, a subtropical bay, and a temperate bay. Amplification occurred in samples from the same site in different seasons and at different depths showing that RNA viruses were widespread and persistent. Sequencing of the amplified gene fragments revealed novel sequences that are highly divergent from any known isolates. The sequences formed a loose cluster together with other RdRP gene fragments derived from temperate seawater, but none of the sequences from the sub-tropical environment were identical to sequences from temperate waters. Phylogenetic analysis suggested that the virotypes from the study represented five new genera and 24 new species of RNA viruses. If it is assumed that all or most of the distinct environmental virotypes have different hosts, the data imply that a diverse assemblage of marine protists may be infected with viruses at any given time. In a more recent study, Gustavsen et al. (2014) examined the temporal and spatial dynamics of picorna-like RNA viruses based on RT-PCR amplification and deep sequencing of the RdRP molecular marker described above in the coastal waters of British Columbia. While greatly expanding the catalogue of picornavirad RdRPs from the marine environment, they found that the community composition of these viruses was extremely variable over time and space. This suggests the hosts of these viruses, likely protists, are subjected only to intermittent attack by this subset of RNA viruses. Single gene surveys based on the amplification of a molecular marker are a useful, sensitive and straightforward means of characterizing the diversity of a particular virus group. However, unlike cellular genomes, viruses do not share a universal gene and thus this method is not appropriate for a global assessment of diversity.

2. Purpose and scope of the review

A number of recent reviews have discussed the application of metagenomic techniques to the investigation of viral ecology in aquatic environments (see Hayes et al., 2017 and Perez-Sepulveda et al., 2016 for example). However none of these have focused exclusively on RNA viromics. The timing of this overview seems appropriate because RNA viruses are starting to be accepted as a ubiquitous and persistent component of the aquatic viroplankton and more sensitive and powerful sequencing and bioinformatic techniques are available that now allow a more comprehensive characterization of RNA from environmental samples. Nevertheless, as will become apparent below, aquatic RNA viromics is a nascent field and there are many fundamental questions about the RNA virus community that remain unanswered. In order to maintain cohesion, I have restricted this review to RNA viruses that infect primarily naturally occurring planktonic microbes in aquatic environments (Table 1). This has resulted in the omission of several studies associated with aquatic environments that employed RNA viromics or detected RNA viruses in a metatranscriptomic-based study, including the characterization of RNA viruses in waste water (Rosario et al., 2009), sewage (Cantalupo et al., 2011; Ng et al., 2012), the

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