

Furtive foes: algal viruses as potential invaders

Janice E. Lawrence

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Viruses are abundant in the world's oceans, existing through parasitic relationships with their various hosts. Algal viruses infect representatives of all major algal taxa, influencing phytoplankton population dynamics, marine foodweb interactions, and global biogeochemical cycling. Although the transportation, spread, and persistence of specific viruses remain to be explored fully, the potential for algal virus introductions and invasions is clearly evident. An estimated 3×10^{22} viruses are transported globally in ballast water alone, destined for ports where few physiological or physical barriers inhibit their invasive success. This fact, coupled with recent findings that viruses are not homogeneously distributed throughout the world's oceans, suggests that virus invasions pose a potential threat to marine ecosystems.

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J. E. Lawrence: *Biology Department, University of New Brunswick, PO Bag Service 45111, Fredericton, NB, Canada E3B 6E1; tel: +1 506 4587842; fax: +1 506 4533583; e-mail: jlawrenc@unb.ca.*

Introduction

The simple but profound importance of algae in marine ecosystems was appropriately emphasized by Kirchman (1999) in the statement, "How phytoplankton die largely determines how other marine organisms live". Phytoplankton form the base of most marine foodwebs, so their growth and death influence oceanic productivity, biogeochemical cycling, and even the global climate. Yet for a long time, oceanographers could not balance the known causes of phytoplankton death against measured phytoplankton growth. Steele (1974) ascribed the discrepancy between primary production and grazing losses to natural death, and although losses attributable to sinking may also be significant, phytoplankton growth rates in many systems even exceed combined losses to grazing and sinking (Kalf and Knoechel, 1978; Walsh, 1983; Reynolds, 1984). This suggests the existence of other loss terms that contribute to reduced primary productivity. In an effort to identify all the processes governing loss terms in phytoplankton population dynamics, Lampert and Sommer (1997) provided the equation $\lambda = \gamma + \sigma + \chi + \delta + \pi + \omega$, where λ is total phytoplankton loss, γ grazing, σ sedimentation, χ competition, δ death or physiological mortality, π parasitism, and ω is washout or advection. This equation describes the rate at which phytoplankton are removed or displaced from aquatic environments, and so do not contribute to the primary productivity of that environment. Research into phytoplankton competition has received great attention and debate; the paradox of the plankton (Hutchinson, 1961) fuelled efforts to understand how many phytoplankton species coexist in a seemingly homogeneous environment such as the sea. Washout and advection have received little attention because the density and distribution of algal populations are too great for these factors to reduce populations significantly (Graham, 2000). However, the remaining means of phytoplankton loss, whether death mediated by parasitism or physiology, have received little attention. Methods were

developed relatively recently that allow us to quantify cellular lysis of phytoplankton (van Boekel *et al.*, 1992; Augusti *et al.*, 1998), leading Brussaard *et al.* (1995) to demonstrate that 75% of phytoplankton die-off at the end of the North Sea spring bloom was attributable to lysis. Nevertheless, pervasive gaps in our understanding of phytoplankton ecology still lie in the few examples and limited understanding we have of algal death. Moreover, our lack of understanding of algal death has ill-prepared us for such emerging concerns as the impacts of invading species on the balance of life and death in the sea.

Abundance and impact of algal viruses

We now know that viruses are extremely abundant, diverse, and ubiquitously distributed in aquatic ecosystems, reaching abundances of 10^8 ml^{-1} in coastal waters (Suttle, 2005) and 10^6 ml^{-1} in the deep sea (Guixa-Boixereu *et al.*, 2002; Ortmann and Suttle, 2005). There they infect all known forms of life and dominate life in the sea numerically; ocean waters are estimated to contain $\sim 4 \times 10^{30}$ viruses (Suttle, 2005). Although the biomass of an individual virus might be considered inconsequential (a virus contains around 0.2 fg of carbon; Suttle, 2005), their sheer abundance translates to a staggering 800 Mt of carbon sequestered in viroplankton. However, biologically speaking, an individual virus is little more than a bit of nucleic acid and protein packaged in a particle smaller than the wavelength of visible light. Viruses have no metabolism of their own; they are obligate pathogens and rely on their host for all metabolic processes, including reproduction. Via lytic or lysogenic life strategies, viruses target specific hosts (often at a subspecies level) and hijack the hosts' cellular machinery to replicate. Progeny are released upon lysis and death of the host.

Many novel, diverse algal viruses have been isolated from aquatic environments. Viruses are known to infect representatives of every major algal phylum, causing cellular lysis upon

completion of each virus life cycle (Lawrence, 2005). Therefore, the life cycles of algal viruses alter phytoplankton clonal diversity (Taruntani *et al.*, 2000; Tomaru *et al.*, 2004) and population density (Bratbak *et al.*, 1993; Brussaard *et al.*, 1996), so influence phytoplankton community succession, primary productivity (Suttle *et al.*, 1990), and ultimately nutrient cycling in the oceans. It is consequently the impacts that viruses have on their hosts and the cascading effects on ecological processes that make viruses of great interest to oceanographers. In essence, how viruses are produced largely explains how other organisms die.

Viruses as non-indigenous species

Non-indigenous species are non-native species that have been transported by human activities to areas where they did not previously occur (Ruiz *et al.*, 2000a). The ultramicroscopic size of viruses greatly facilitates their widespread transport in water, sediments, biofilms, and inside infected hosts. Several studies have confirmed the potential for viral introductions through ship ballast water and biofilms; the number of virus-like particles (VLPs) in ship ballast, ballast sediment, and biofilms are of the order of 10^7 , 10^9 , and 10^9 ml^{-1} , respectively (Ruiz *et al.*, 2000b; Drake *et al.*, 2002a, b, 2005, 2007; Wilhelm *et al.*, 2006). Although the total volume of ballast sediment and ship biofilm transported through shipping is relatively small, between 3 and 4 billion tonnes of ballast water are transported globally each year (Endresen *et al.*, 2003). Therefore, some 3×10^{22} VLPs are discharged into foreign ports by ballast alone, revealing an enormous potential for introductions of non-indigenous viruses. Coupled with the potential for transfer of infected phytoplankton cells, Brussaard *et al.* (1996) observed that up to 50% of cells in a bloom of *Emiliania huxleyi* were visibly infected), there is little doubt that viruses are spread to the far reaches of the globe via shipping activities.

Algal virus introductions

There are few physiological barriers limiting the introduction of viruses to new habitats. Free viruses are dormant and may remain in the environment until they find a suitable host or are removed by other processes. As they have no metabolism, virus introductions are not as constrained by time or limited to certain modes of transport as metabolically active organisms. Deactivation, whether through decay by solar radiation (Suttle and Chen, 1992) or biochemical conditions (Noble and Fuhrman, 1997), and grazing by nanoflagellates (González and Suttle, 1993) are presumably the only mechanisms by which viruses are lost. The rates of decay and deactivation are highly variable among algal viruses isolated to date. For example, *Heterosigma akashiwo* Virus and *Heterocapsa circularisquama* Virus are susceptible to rapid deactivation under cool, dark conditions, and *Heterocapsa circularisquama* RNA Virus remains stable under the same conditions (Tomaru *et al.*, 2005). Even among different strains of the same virus, decay rates may be variable, as demonstrated by the temperature sensitivity of different *Phaeocystis globosa* Virus strains (Baudoux and Brussaard, 2005). This indicates that the potential for successful introduction of algal viruses is virus-specific.

Viruses displaced from a particular location through ballast water transfer, advection, or sedimentation via adsorption onto sinking particles may remain dormant for long periods. In fact, viruses adsorbed onto sediments have greatly decreased inactivation rates in seawater (LaBelle and Gerba, 1980, 1982; Rao

et al., 1984), likely explaining why infectious algal viruses exist in sediments that were deposited between tens and hundreds of years ago (Suttle, 2000; Lawrence *et al.*, 2002). Therefore, in addition to the potential for initial introduction through free viruses and infected hosts in ballast water, biofilms, and ballast tank sediments, viruses that have been displaced to the benthos via sedimentation may be chronically reintroduced into foreign environments through dredging and other man-made and natural resuspension events, thus greatly extending the window of opportunity for viral invasions. Moreover, the rapid distribution of viruses throughout the marine environment may increase the geographical range of initial viral introductions. The alongshore dispersal rate of herpes virus among pilchard may exceed $10\,000 \text{ km year}^{-1}$ (Murray *et al.*, 2001), and morbillivirus among seal and dolphin populations $3000 \text{ km year}^{-1}$ (Heide-Jorgensen and Härkönen, 1992; Aguilar and Raga, 1993). Such rapid dispersal is most likely explained by the relative lack of physical barriers in the ocean, and strong, directional, one-dimensional flow along coastlines (McCallum *et al.*, 2003).

Algal virus invasions

After introduction, successful viral invasions require access to a suitable host population because they cannot reproduce outside their host. The geographical range of potential host algae and the host range of the introduced virus are important for assessing the potential for invasion success. Theoretically, without considering any biases introduced by the mode of introduction such as shipping patterns for ballast water transfers, viruses that infect cosmopolitan species pose a greater potential for invasion because they are more likely to encounter a suitable host in a new environment. Algal viruses have been isolated that infect cosmopolitan species such as the prasinophytes *Micromonas pusilla* (Cottrell and Suttle, 1995; Brussaard *et al.*, 2004) and *Pyramimonas orientalis* (Sandaa *et al.*, 2001), and the prymnesiophytes *Chrysochromulina ericina* (Sandaa *et al.*, 2001) and *E. huxleyi* (Castberg *et al.*, 2002), more narrowly distributed species such as *H. akashiwo* (Nagasaki and Yamaguchi, 1997; Lawrence *et al.*, 2001; Tai *et al.*, 2003) and *P. globosa* (Baudoux and Brussaard, 2005), which are restricted to temperate and Subarctic waters, and *Heterocapsa circularisquama*, which is believed to be restricted to coastal and western Japanese waters (Taruntani *et al.*, 2001). This indicates that the potential for invasion as well as the potential for introduction are virus-specific.

Viruses with broad host ranges are more likely to encounter appropriate hosts upon introduction to new environments than viruses with narrow host ranges. The host ranges of most algal viruses isolated to date are limited to an individual species and do not extend to other phyla or even closely related species within a phyla (Table 1). One notable exception is the susceptibility of both *Chrysochromiluna brevivifilum* and *C. strobilis* to *Chrysochromulina brevivifilum* Virus (Suttle and Chan, 1995). In fact, for all other algal viruses examined, host range is often limited to strains within a species that were isolated from the same geographic region as the virus (Table 2). Although this suggests that the potential for an algal virus invasion is low, it is important to note that some viruses were able to infect strains of algal species from different ocean basins (e.g. *P. globosa* strain Pg Kac31, which was isolated from Northeastern Pacific coastal waters, is susceptible to lytic infection by *P. globosa* Virus strain 01T, which was isolated from the North Sea; Baudoux and Brussaard, 2005). This picture is further complicated because

Table 1. Summary of interphyla algal–virus host range studies.

Virus	Identified host ^a (Host Phylum)	Phyla of screened representatives	Susceptibility of representatives	Reference
CeV	<i>Chrysochromulina ericina</i> (Prymnesiophyceae)	Bacillariophyceae	–	Sandaa <i>et al.</i> (2001)
		Chrysophyceae	–	
		Cryptophyceae	–	
		Cyanophyceae	–	
		Dinophyceae	–	
		Prymnesiophyceae	+ ^b	
		Prasinophyceae	–	
CsNIV	<i>Chaetoceros salsauginium</i> (Bacillariophyceae)	Bacillariophyceae	+ ^b	Nagasaki <i>et al.</i> (2005)
		Chlorophyceae	–	
		Eustimatophyceae	–	
		Raphidophyceae	–	
CspNIV	<i>Chaetoceros cf. gracilis</i> (Bacillariophyceae)	Bacillariophyceae	+ ^b	Bettarel <i>et al.</i> (2005)
		Dinophyceae	–	
		Prasinophyceae	–	
EhV	<i>Emiliana huxleyi</i> (Prymnesiophyceae)	Prymnesiophyceae	+ ^b	Castberg <i>et al.</i> (2002)
		Prasinophyceae	–	
HaV	<i>Heterosigma akashiwo</i> (Raphiophyceae)	Bacillariophyceae	–	Nagasaki and Yamaguchi (1997)
		Chlorophyceae	–	
		Cryptophyceae	–	
		Dinophyceae	–	
		Prasinophyceae	–	
		Prymnesiophyceae	–	
		Raphidophyceae	+ ^b	
HcV	<i>Heterocapsa circularisquama</i> (Dinophyceae)	Bacillariophyceae	–	Taruntani <i>et al.</i> (2001)
		Chlorophyceae	–	
		Cryptophyceae	–	
		Dinophyceae	+ ^b	
		Euglenophyceae	–	
		Prymnesiophyceae	–	
		Raphidophyceae	–	
MpRNAV	<i>Micromonas pusilla</i> (Prasinophyceae)	Cryptophyceae	–	Brussaard <i>et al.</i> (2004)
		Cyanophyceae	–	
		Dinophyceae	–	
		Prasinophyceae	+ ^b	
		Prymnesiophyceae	–	
PoV	<i>Pyramimonas orientalis</i> (Prasinophyceae)	Bacillariophyceae	–	Sandaa <i>et al.</i> (2001)
		Chrysophyceae	–	
		Cryptophyceae	–	
		Cyanophyceae Dinophyceae	–	
		Prymnesiophyceae	–	
		Prasinophyceae	+ ^b	
PgV	<i>Phaeocystis globosa</i> (Prymnesiophyceae)	Bacillariophyceae	–	Baudoux and Brussaard (2005)
		Chlorophyceae	–	
		Cryptophyceae	–	

Continued

Table 1. Continued

Virus	Identified host ^a (Host Phylum)	Phyla of screened representatives	Susceptibility of representatives	Reference
		Cyanophyceae	–	
		Dinophyceae	–	
		Eustimatophyceae	–	
		Prasinophyceae	–	
		Prymnesiophyceae	+ ^b	
RsRNAV	<i>Rhizosolenia setigera</i> (Bacillariophyceae)	Bacillariophyceae	+ ^b	Nagasaki <i>et al.</i> (2004)
		Chlorophyceae	–	
		Dinophyceae	–	
		Euglenophyceae	–	
		Eustimatophyceae	–	
		Raphidophyceae	–	

^aThe identified host is the one used to isolate the virus, ^bThe only representative of these phyla that were susceptible to infection was strains of the identified host species.

Table 2. Summary of interspecies algal–virus host range studies.

Virus and origin	Identified algal host	Origin of algal strain	Susceptibility of algal strain*	Reference
CeV Norwegian coastal waters	<i>Chrysochromulina ericina</i>	North Pacific Ocean Norwegian coastal waters	1– 3+	Sandaa <i>et al.</i> (2001)
EHV Norwegian coastal waters	<i>Emiliania huxleyi</i>	Norwegian coastal waters	3+	Castberg <i>et al.</i> (2002)
HaNIV NE Pacific coastal waters	<i>Heterosigma akashiwo</i>	NE Pacific coastal waters NW Atlantic coastal waters Japanese coastal waters	4+, 3– 4– 2–	Lawrence <i>et al.</i> (2001)
HaRNAV NE Pacific coastal waters	<i>Heterosigma akashiwo</i>	NE Pacific coastal waters NW Atlantic coastal waters Japanese coastal waters	3+, 4– 4– 2+, 2–	Tai <i>et al.</i> (2003)
HaV Nomi Bay, Kochi Prefecture, Japan	<i>Heterosigma akashiwo</i>	Gakasho Bay Hiroshima Bay Hiroshima Bay Hiroshima Bay Uranouchi Bay	1+ 1– 1– 1– 1+	Nagasaki and Yamaguchi (1997)
MpRNAV Norwegian coastal waters	<i>Micromonas pusilla</i>	Norwegian coastal waters NW Atlantic coastal waters NE Atlantic coastal waters	1+ 1– 4–	Brussaard <i>et al.</i> (2004)
PgV Group 1 Group 2A Group 2B Group 2C Southern Bight, North Sea	<i>Phaeocystis globosa</i>	Southern Bight, North Sea Unknown NE Pacific coastal waters Norwegian coastal waters	PgV 1: 4+, 5– PgV 2A&B: 5+, 4– PgV 2C: 9+ PgV 1, 2A&B: – PgV 2C: + PgV 1, 2A&B: – PgV 2C: + PgV 1, 2A&B: – PgV 2C: +	Baudoux and Brussaard (2005)
PoV Norwegian coastal waters	<i>Pyramimonas orientalis</i>	Norwegian coastal waters	1+, 1–	Sandaa <i>et al.</i> (2001)
PpV Norwegian coastal waters	<i>Phaeocystis pouchetii</i>	Norwegian coastal waters	2+	Jacobsen <i>et al.</i> (1996)

x⁺ indicates that the virus causes lysis in x strains of algae from the region indicated, y– indicates that the virus did not cause lysis in y strains of the algae from the region indicated.

global transfers of algae and viruses began before we started studying them; we currently do not know what the geographic distribution of algal viruses and susceptible algal species would be without the human influence to date. Moreover, phytoplankton species definitions are being refined through the development and application of molecular tools and will likely reshape our current concept of the host range of algal viruses.

In addition to finding a suitable host, there exists the potential for host shifts. Although not yet documented among algal viruses, the potential for a virus' host range to shift upon exposure to a new host has been documented. It is believed that canine distemper virus was introduced to Antarctic seal populations through exposure to sled dogs (Bengston *et al.*, 1991), and that influenza virus introduced through aquatic and migratory birds is responsible for seal and whale mortality (Geraci *et al.*, 1982).

Distribution of algal viruses

The possibility of algal virus introductions and invasions through any means would not be a concern if viruses were homogeneously mixed throughout the world's oceans. Although the prevailing paradigm has been that everything is everywhere and, therefore, no virus can be non-indigenous, recent findings suggest that this is not the case. In a metagenomic analysis of viral assemblages from four major oceanic regions, Angly *et al.* (2006) found a significant difference between phages from different oceanic regions and a significant positive correlation between geographic distance (in km) and genetic distance (in Φ_{ST}). This finding was echoed in studies of RNA viruses by (Culley *et al.* 2003, 2006), where large differences were found in the RNA virus assemblages at two locations, with no discernible overlap between the assemblages. Circumstantial evidence of the restricted distribution of algal viruses also exists; whereas the alga *H. akashiwo* forms blooms on either side of the Pacific Ocean, *H. akashiwo* Nuclear Inclusion Virus (HaNIV), *H. akashiwo* RNA Virus (HaRNAV), and a *H. akashiwo* 2-virus system (Ha2V) have only been isolated from the eastern Pacific (Lawrence *et al.*, 2001, 2002; Tai *et al.*, 2003), and *H. akashiwo* virus (HaV) appears to be limited to the western Pacific (Nagasaki and Yamaguchi, 1997, 1998).

Looking forward

The potential for viral introductions to new environments is both apparent and probable. The sheer abundance of viruses, especially in the coastal waters that serve as sources of ballast water, ease of transfer, and lack of physical and physiological barriers suggest that algal viruses are well positioned for successful invasion. To gain a better understanding of the potential for specific algal virus invasions, we need a more thorough collection of the algal viruses that exist and further studies into their characteristics, such as their host ranges, biochemical tolerances, phylogenetic relationships with other viruses, geographical distribution, genetic diversity, and potential for host shifts. Further, it is essential that we produce a comprehensive catalogue of algal species and their geographic distributions so that we can overlay potential vectors for introduction with populations of susceptible hosts. Finally, we must begin thinking about mitigating viral introductions and investigate the efficacy of current methods, such as mid-ocean exchange of ballast water, at reducing or eliminating the potential for virus introduction.

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