



Short communication

Virio plankton distribution and activity in a tropical eutrophicated bay

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ABSTRACT

The study of lysogeny in aquatic systems is an often overlooked aspect of microbial ecology, especially in tropical environments. Herein, the fraction of lysogenized cells (FLC) was detected in the surface waters of 20 coastal stations distributed from the eutrophicated shoreline to seaward waters of Hann Bay (Senegal). Concurrently, viral lytic infection rates were extrapolated from the frequency of visibly infected bacterial cells (FVIC), as determined from transmission electron microscopy observations. The experimental induction of prophage was observed in less than 3% of indigenous marine bacteria, suggesting that lysogenic stages of infection are rare in Hann Bay. Similarly, only 0.5–4.7% of bacteria showed visible signs of lytic infection. However, the positive correlation between the fraction of lysogenic and lytic cells ($r = 0.67$, $p < 0.05$, $n = 20$) may actually indicate that the coexistence of both lifestyles may be due to the massive and rapid induction of lysogens, potentially from the high levels of local UV radiation. Overall, we suggest that the determination of FVIC and FLC to examine the predominance of one type of cycle versus the other may be a source of misinterpretation in some particular aquatic environments.

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1. Introduction

Planktonic viruses are now unarguably viewed as essential components of aquatic environments with regard to their natural abundance and their multiple biogeochemical and ecological functions (Fuhrman, 1999; Suttle, 2007). By primarily targeting prokaryotes, viruses can interact with their hosts in two major and distinctive ways, lytic and lysogenic stages of infection, and more sporadically through pseudolysogeny (Williamson et al., 2001).

One of the most important roles of viruses in aquatic systems is their ability to act as vectors for transferring genes, and lysogeny is a key mechanism in this process (Weinbauer, 2004). Lysogeny occurs when the viral genome integrates into any replicon of the host bacterium and replicates together with it. No progeny viruses are initially produced (except rare ones from spontaneous induction). Instead, the infecting virus remains quiescent within the bacterium's chromosome until exposure to specific stimuli, such as solar radiation (Weinbauer and Suttle, 1999), pollutants (Cochran et al., 1998), or changes in temperature (Wilson et al., 2001), salinity

(Cissoko et al., 2008) and nutrient regimes (Mcdaniel and Paul, 2005). Following this induction event, the virus enters a lytic life cycle in which its genome is extracted from the host chromosome and begins to replicate, producing new progeny viruses. Ultimately the cell host is lysed and the viral particles are released into the environment, where they infect new bacterial cells. Thus, although data are limited, they seem to suggest that the lysogenic-lytic shift may be the result of viral genes responding to a complex interplay of physiological and environmental cues (Weinbauer et al., 2003; Paul and Sullivan, 2005).

Mitomycin c is an antibiotic of the family of aziridine and represents, along with UV-C radiation (<300 nm), one of the most powerful inducing agents (Weinbauer, 2004). Prevalence of lysogeny, determined after mitomycin addition has been shown to be highly variable across aquatic environments. Lysogenized bacteria were observed at proportions of (a) less than 10% in temperate lakes (Colombet et al., 2006) and coastal seawaters (Weinbauer and Suttle, 1999), (b) from 10% to 50% in offshore waters (Jiang and Paul, 1996; Bongiorni et al., 2005), and (c) from 50% to 100% in estuaries (Cochran and Paul, 1998), Antarctic saline lakes (Laybourn-Parry et al., 2007) and deep marine waters (Weinbauer et al., 2003). Interestingly, in temperate areas where lytic versus lysogenic stages of infection was examined

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concurrently in natural populations of marine and freshwater bacteria, the two viral life cycles showed a tendency to exclude each other (Weinbauer et al., 2003; Colombet et al., 2006).

The factors that trigger the lysogenic decision in the bacterioplankton remain uncertain although literature tends to show that lysogeny is favoured during times of low resources, low host abundance and low growth rate (Williamson et al., 2002; Long et al., 2008). Recently, we have reported low fraction of lysogenized bacterial cells in the surface layer of a variety of water bodies, arguing that the combination of promoting growth conditions for the hosts as well as the high irradiance was thought to explain the quasi absence of lysogenized cells (Bettarel et al., 2006). Lysogeny is now commonly viewed as a survival strategy of phages at times of adverse conditions for their proliferation, whilst also conferring immunity to infection by related viruses (Ackermann and Dubow, 1987).

The main goal of this research was therefore to explore the co-occurrence of the two life strategies of tropical marine viruses along a trophic gradient, to tentatively determine whether both cycles are mutually exclusive or whether they may coexist and covary. Twenty coastal stations were sampled in Hann Bay, located in Senegal (West Africa). The stations were distributed throughout the bay from the heavily human impacted shoreline (eutrophic conditions) (Bouvy et al., 2008) to offshore waters (oligotrophic conditions), and were thus naturally exposed to strong stimuli (UV, pollutants, nutrients) for the induction of prokaryotic lysogens.

2. Materials and methods

Samples were collected on 9 and 10 November, 2004 between 10:00 h and 12:00 h in Hann Bay (Senegal) located beneath the Cap-Vert Peninsula, which hosts the whole population of the main Senegalese city, Dakar (around three million inhabitants including its suburbs). This bay receives up to 80% of the waste of Senegalese industries and probably represents one of the largest polluted sites of West Africa (www.blacksmithinstitute.org). Twenty coastal stations were sampled within the bay as follows: eleven were located all along the heavily polluted near-shore

waters (N#1 → N#11), six others at intermediate distances from the shore line (I#1 → I#6) and three seaward stations (S#1 → S#3) (Fig. 1). Water samples were collected with acid-cleaned sterile bottles at 0.5 m below the surface, at the different stations. Triplicate sub-samples were analysed for nutrient and chlorophyll contents, as well as for bacterial and viral parameters. Samples for dissolved inorganic nutrient measurements ($\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$) were previously filtered through Whatman GF/F fibreglass filters, stored at -20°C and analysed according to Strickland and Parsons, 1968. Chlorophyll-*a* (Chl) concentrations were determined fluorometrically following filtration of samples onto Whatman GF/F filters, and methanol extraction (Yensch and Menzel, 1963). Oxygen concentrations were measured *in situ* using a YSI probe with temperature correction.

Viral subsamples were fixed with 0.02 μm filtered buffered formaldehyde (final concentration 2% v/v) after sampling, immediately flash frozen in liquid nitrogen and stored at -80°C prior to counting, according to Wen and collaborators' recommendations (Wen et al., 2004). The number of virus-like particles (VLPs) in triplicate 0.5- to 1-mL samples were determined after retention of the particles on 0.02- μm pore size membranes (Anodisc) and staining with SYBR Gold fluorochrome (Molecular Probes, Europe, Leiden, Netherlands) as described by Chen et al. (2001). For determination of total bacterioplankton, triplicate 2-mL samples were fixed with 0.2 μm filtered buffered formaldehyde (final concentration 2% v/v), stained with DAPI fluorochrome and filtered onto 0.2- μm pore-size polycarbonate membranes. Heterotrophic bacterial production (HBP) was estimated by the [^3H]thymidine incorporation method as developed by Fuhrman and Azam (1982). For each sample, two 3-mL replicates and one control (0 time) were incubated with 100 μL of [^3H]thymidine (final concentration 20 nM, specific activity = 47 Ci mmol^{-1} , Amersham, Little Chalfont, UK) and held in the dark for 15 min at *in situ* temperature. Radioactivity was counted using the liquid scintillation procedure. Bacterial production was calculated from the radioactivity incorporated in trichloroacetic acid (TCA) precipitate, using a conversion factor of 1.96×10^{18} cells produced per mole of incorporated thymidine reported in tropical ecosystems (Pradeep Ram et al., 2007). For viral

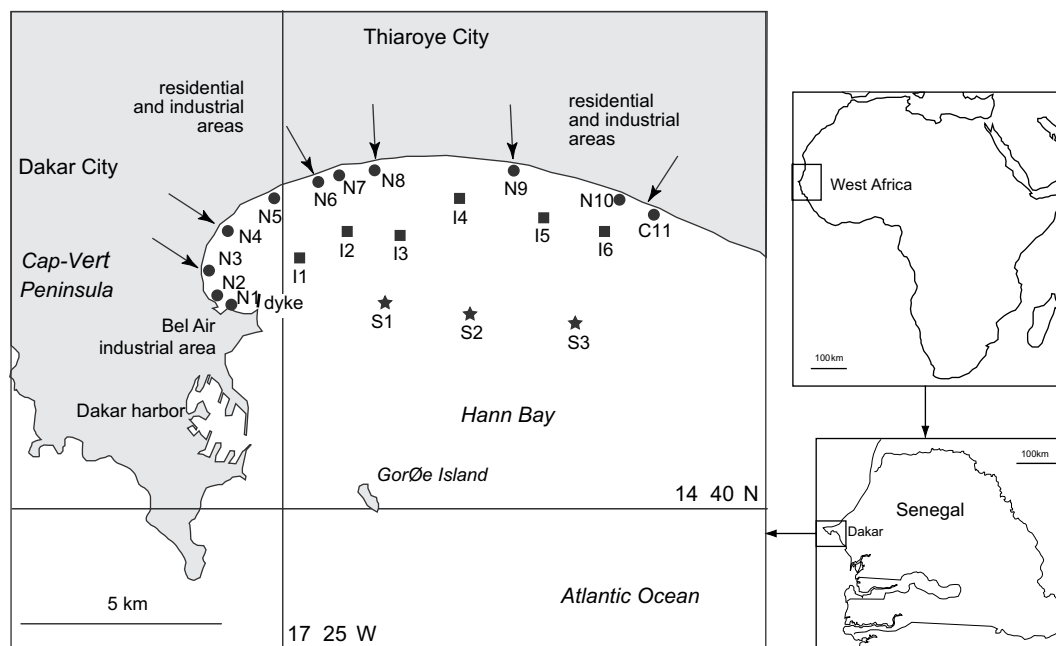


Fig. 1. Map of Senegal (West Africa) and locations of the 20 sampling stations. N, near-shore stations; I, intermediate stations; S, seaward stations. Dark arrows indicate sewage discharge sites.

lytic infection, the viral-induced bacterial mortality (VIBM) was calculated from the frequency of visibly infected cells (FVIC) obtained from observations under a JEOL 1200EX transmission electron microscope (TEM), following ultracentrifugation and uranyl acetate staining. The procedure is detailed elsewhere (Bettarel et al., 2004). For each duplicate sample, mean burst size was estimated from the number of viruses in those infected cells which were filled with phages. The frequency of lysogenically infected cells (FLC) was determined from the induction of prophages using mitomycin C (Weinbauer et al., 2003). Mitomycin c was added to samples (final concentration $1 \mu\text{g mL}^{-1}$) in 20-mL sterile serum bottles, and untreated samples served as controls. Samples were incubated at *in situ* temperature; duplicate subsamples were removed with syringes at t0 and t12 h and fixed with 0.02 μM filtered buffered formaldehyde (2% final concentration) for viral and bacterial counts. FLC was estimated from viral abundances in mitomycin C treated (VAm) and control (VAc) incubations, and bacterial abundance (BA_{t0}) and burst size (BS_{t0}) in original samples: $\text{FLC} = 100[(\text{VAm} - \text{VAc})/(\text{BS}_{t0} \times \text{BA}_{t0})]$, (Weinbauer et al., 2003).

3. Results and discussion

Although temperature was comparable at all sampling stations (between 24 and 26 °C), oxygen and nutrient concentrations were highly variable with regards to the proximity to the shore line, with the lowest levels of oxygen and highest concentrations of chlorophyll-*a* and dissolved inorganic nutrients (PO_4 , NO_3 , NH_4) being recorded at the near-shore (N) polluted stations. Unsurprisingly, the opposite trend was recorded at seaward stations (S) where coastal nutrients have been diluted. Intermediate stations (I) were characterized by transitional concentrations in oxygen, nutrients and chlorophyll-*a* (Table 1).

As expected, viral and bacterial abundances naturally decreased from the shore toward the open ocean (Table 2). Burst sizes of infected cells were, on average, also slightly (but not significantly) higher at near-shore (mean = 33.5, coefficient of variation: $\text{cv} = 35.8\%$) than at seaward stations (mean = 26.2, $\text{cv} = 36.7\%$). This parameter was positively correlated with bacterial production ($r = 0.51$, $p < 0.05$, Table 3), supporting the observations that BS generally increases with the organic load of the environment (Bettarel et al., 2004; Parada et al., 2006). One of the most striking observation of our study is the very low virus-to-bacteria ratio that

ranged between 0.6 and 3.2 (mean = 1.8, Table 2), i.e. among the lowest values reported in the literature (Weinbauer, 2004). Interestingly, similar atypical ratios were found in a parallel study conducted in a variety of aquatic inland sites of the same region of West Africa (Bettarel et al., 2006). Such low VBRs can not be considered as the result of underestimated virus concentrations due to a methodological bias, as recommendations provided by Wen et al. (2004) were strictly followed to obtain accurate and reproducible estimates of viral abundance.

There are at least four basic scenarios that may be envisioned to explain the low VBRs: (1) low infection capacities of planktonic viruses due to host resistance or inactivation by environmental factors, (2) viral deterioration by UV radiation, (3) prevalence of lysogenic over lytic stages of infection, (4) low bacterivorous and/or high virivorous activities of protists (Gonzalez and Suttle, 1993; Bettarel et al., 2005).

Scenario 1 did not appear to be supported by our results since TEM examinations revealed that 0.5–4.7% of bacterial cells were containing phages (mean = 1.4%, $\text{cv} = 79.1\%$) (Table 2). For the rest, those values are likely to be minimum estimates as frequencies of virally infected prokaryotes have been reported to be the lowest around noon (Bettarel et al., 2002; Winter et al., 2004), the sampling time chosen in the present study. Unlike West African inland waters where FVIC were remarkably low (mean, 0.5%) (Bettarel et al., 2006), the values found in Hann Bay are within the range of what is commonly detected in temperate marine environments (Weinbauer, 2004). Therefore, marine prokaryotes in this bay were not specifically resistant to viral attack.

Scenario 2 is conceivable given the high levels of local irradiance that may cause extensive photo-oxidative damage on viral stocks under tropical latitudes (Bettarel et al., 2006). However, the ability of viruses to resist to highly irradiated environments like the Sahara desert (Prigent et al., 2001) or the superficial sea microlayer (Joux et al., 2006) raises numerous questions about sunlight adaptation and persistence of phages in aquatic and terrestrial environments.

Scenario 3 assumes that the low VBR may result from widespread lysogenic infections thus limiting the pool of free viruses in the water. Indeed, if lysogeny represents a beneficial strategy when rates of contact between hosts and viruses are low (Weinbauer and Suttle, 1999) then low virus-to-bacteria ratio (which can be considered as a proxy for contact possibilities between a phage and its bacterial hosts) should favour lysogenic

Table 1

Geographical coordinates and physico-chemical parameters of the 20 stations sampled in Hann Bay, November 2004. N, near-shore stations; I, intermediate stations; S, seaward stations

Station	Latitude North	Longitude West	Oxygen (mg L^{-1})	PO_4 (μM)	$\text{NO}_3^- + \text{NO}_2^-$ (μM)	NH_4^+ (μM)	Chl <i>a</i> ($\mu\text{g L}^{-1}$)
N#1	14° 42.430'	17° 25.570'	2.9	4.5	5.8	21.7	8.6
N#2	14° 42.575'	17° 25.757'	1.9	4.2	1.7	31.9	17.2
N#3	14° 42.895'	17° 25.840'	1.6	35.6	1.7	210.0	15.6
N#4	14° 43.431'	17° 25.619'	2.5	2.6	1.1	5.8	5.9
N#5	14° 43.909'	17° 25.035'	2.6	2.5	1.5	6.6	6.5
N#6	14° 44.116'	17° 24.360'	5.9	6.2	0.6	1.8	21.3
N#7	14° 44.138'	17° 24.328'	5.0	6.5	0.4	2.3	16.4
N#8	14° 44.272'	17° 23.860'	5.9	5.2	4.6	3.0	50.4
N#9	14° 44.369'	17° 22.197'	3.6	8.5	4.4	5.6	61.4
N#1	14° 44.164'	17° 20.925'	4.4	52.3	4.8	64.2	34.5
N#1	14° 44.104'	17° 20.655'	4.3	78.9	4.3	118.5	37.0
I#1	14° 43.160'	17° 24.700'	6.1	10.6	3.1	6.2	9.8
I#2	14° 43.530'	17° 24.190'	5.5	9.0	1.9	5.2	8.3
I#3	14° 43.790'	17° 23.550'	6.3	7.0	1.0	3.7	13.3
I#4	14° 43.900'	17° 22.830'	5.5	2.6	0.6	1.2	5.7
I#5	14° 43.810'	17° 21.990'	6.5	0.7	0.3	0.2	3.1
I#6	14° 43.620'	17° 21.130'	5.8	8.4	1.5	4.3	9.8
S#1	14° 42.800'	17° 23.690'	6.8	0.8	0.3	0.1	2.3
S#2	14° 43.080'	17° 22.720'	6.6	0.9	0.5	0.2	4.4
S#3	14° 42.880'	17° 21.650'	7.1	1.2	0.9	1.7	5.0

Table 2

Viral and microbial parameters in surface waters of Hann Bay in November 2004. N, near-shore stations; I, intermediate stations; S, seaward stations

Station	[Viruses] (10^7 mL^{-1})	[Bacteria] (10^6 mL^{-1})	VBR	HBP ($10^7 \text{ cells L}^{-1} \text{ h}^{-1}$)	FVIC (%)	VIBM (%)	Burst size	FLC (%)
N#1	1.7 ± 0.3	10.9 ± 1.4	1.5	51.5 ± 3.3	1.5 ± 0.5	12.9 ± 4.3	29.5 ± 10.4	0.9 ± 0.2
N#2	1.3 ± 0.3	9.7 ± 0.7	1.4	46.7 ± 2.2	1.0 ± 0.1	8.0 ± 0.8	54.6 ± 23.2	0.2 ± 0.05
N#3	2.2 ± 0.4	22.3 ± 3.1	1.0	118.6 ± 7.4	0.6 ± 0.3	4.8 ± 2.4	50.0 ± 10.2	0.6 ± 0.1
N#4	1.1 ± 0.2	5.1 ± 0.6	2.2	18.9 ± 0.8	0.9 ± 0.7	7.1 ± 5.5	22.5 ± 5.2	2.0 ± 0.7
N#5	2.7 ± 0.1	12.7 ± 2.0	2.1	28.3 ± 1.8	0.8 ± 0.1	6.1 ± 0.8	19.0 ± 3.1	0.1 ± 0.01
N#6	1.6 ± 0.1	8.6 ± 1.1	1.9	15.9 ± 1.6	0.8 ± 0.3	6.0 ± 1.3	39.2 ± 7.8	0.0 ± 0.0
N#7	1.5 ± 0.2	6.4 ± 0.5	2.3	11.8 ± 0.7	0.9 ± 0.2	6.9 ± 2.4	40.0 ± 10.1	0.0 ± 0.0
N#8	1.6 ± 0.3	9.6 ± 1.0	1.7	22.8 ± 1.6	4.7 ± 1.6	67.0 ± 11.2	37.4 ± 6.8	3.0 ± 0.4
N#9	1.2 ± 0.1	16.0 ± 2.3	0.8	32.5 ± 2.6	3.6 ± 0.6	4.1 ± 12.0	16.7 ± 5.8	2.3 ± 0.8
N#10	1.8 ± 0.2	6.6 ± 0.4	2.7	18.0 ± 1.0	0.7 ± 0.2	5.0 ± 1.0	38.0 ± 10.1	0.0 ± 0.0
N#11	0.3 ± 0.0	5.0 ± 0.8	0.6	10.0 ± 0.1	0.5 ± 0.1	3.9	22.0 ± 5.6	1.4 ± 0.5
Mean	1.6	10.3	1.7	34.1	1.4	15.4	33.5	1.0
I#1	0.5 ± 0.1	3.7 ± 0.5	1.2	10.3 ± 0.5	0.6 ± 0.2	4.4 ± 1.5	24.2 ± 6.2	0.6 ± 0.2
I#2	0.9 ± 0.1	4.1 ± 0.5	2.1	9.5 ± 1.1	1.1 ± 0.7	8.8 ± 5.6	16.5 ± 2.6	0.6 ± 0.1
I#3	0.6 ± 0.2	3.6 ± 0.3	1.8	5.9 ± 0.4	2.5 ± 0.2	25.0 ± 2.0	21.8 ± 3.8	1.0 ± 0.3
I#4	0.3 ± 0.0	2.9 ± 0.2	1.1	5.2 ± 0.4	0.8 ± 0.5	6.1 ± 3.8	39.0 ± 11.4	1.1 ± 0.2
I#5	0.7 ± 0.1	2.7 ± 0.3	2.7	2.9 ± 0.1	2.0 ± 0.3	18.6 ± 2.8	16.4 ± 10.8	0.0 ± 0.0
I#6	0.7 ± 0.2	2.3 ± 0.3	3.1	2.5 ± 0.5	2.0 ± 0.1	18.3 ± 0.9	24.2 ± 11.1	0.1 ± 0.03
Mean	0.6	3.2	2.0	6.0	1.5	13.5	23.7	0.6
S#1	0.4 ± 0.1	2.3 ± 0.2	1.8	2.1 ± 0.1	1.0 ± 0.3	8.1 ± 2.4	14.0 ± 3.8	0.5 ± 0.05
S#2	0.7 ± 0.1	2.1 ± 0.3	3.2	5.6 ± 0.3	0.9 ± 0.3	7.0 ± 2.3	37.5 ± 11.4	0.1 ± 0.02
S#3	0.4 ± 0.0	3.1 ± 0.4	1.4	0.8 ± 0.1	0.6 ± 0.1	4.7 ± 0.1	27.0 ± 3.0	0.0 ± 0.0
Mean	0.5	2.5	2.1	2.8	0.8	6.6	26.2	0.2

decision (Weinbauer, 2004). In Hann Bay, the presence of temperate bacteriophages was assessed by inducing the presumed lysogens with mitomycin c. With an average of 0.6% of inducible bacteria in the different stations (min.–max. 0–3%), lysogeny, did not yet emerge as a dominant strategy for virus proliferation in this ecosystem. However, these results can be considered as minimum estimates, as mitomycin c does not consistently induce all prophages (Ackermann and Dubow, 1984). Lysogenic bacteriophages are typically insignificant in coastal waters (Weinbauer and Suttle, 1999). In addition, such ranges of values were previously found in Senegalese freshwaters (min.–max. 0.1–7.1%) (Bettarel et al., 2006), and in the temperate Lake Erie (Tapper and Hicks, 1998). In Hann Bay, which is characterized by a eutrophic shoreline, prokaryotes are abundant and highly active, with production ranging from 10.0 to 118.6×10^7 cells $\text{L}^{-1} \text{h}^{-1}$ (mean = 34.1×10^7 cells $\text{L}^{-1} \text{h}^{-1}$; Table 2). Therefore, the quasi absence of detectable lysogens in our study is not surprising. The high levels of local tropical UV radiation may also help explain the low fraction of lysogens. Indeed, in their comprehensive study on lysogeny, Weinbauer et al. (2003) reported that the lowest virus-to-bacteria ratios measured in the deep dark waters of the Mediterranean Sea (1.1–5.6) were associated with the highest frequencies of lysogenic cells (mean, 73.2%). In Hann Bay surface water, conversely to the deep dark Mediterranean waters, bacteria were highly exposed to local light

conditions, including UV radiation which represents a powerful environmental inducing agent (Weinbauer et al., 1999). Therefore, one may suspect that the weak proportion of lysogens detected in Hann Bay after mitomycin c addition may be partly explained by the fact that a fraction of lysogenized cells were already activated by natural light. Although this view is speculative as sub-surface UV radiation was not measured, it seems to be supported by the observation that FLCs, for the whole sampling site, were positively correlated with those of FVIC ($r = 0.67$, $p < 0.05$, $n = 20$) (Table 3). In temperate areas, few studies have confronted lytic versus lysogenic strategies in the marine (Weinbauer et al., 2003) and freshwater environment (Colombet et al., 2006), but in all cases, FVIC and FLC were inversely correlated, suggesting that 'environments exist where one of the two viral life strategies prevails' (Weinbauer et al., 2003). Here, the positive correlation of both stages of infection may imply a continuous induction of a fraction of the lysogens from natural conditions, with cells identified as virally infected in TEM (in a lytic cycle) being formerly lysogens. Hence, mitomycin c, under certain circumstances, may only induce the fraction of residual lysogens that was not formerly induced by environmental factors. Although the difference is not statistically significant (t -test, unequal sample sizes, unequal variance), the fact that FLC was lower at seaward (mean = 0.2%) than at near-shore stations (mean = 1%) seems to suggest that where light penetration is

Table 3Correlation relationships of environmental parameters in Hann Bay. Significant correlations are indicated in bold as follows: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

	PO ₄	NH ₄	NO ₃ + NO ₂	[O ₂]	Chl a	[Bact.]	[VLP]	BP	FVIC	BS
NH ₄	0.73***									
NO ₃ + NO ₂	0.48*	0.25								
[O ₂]	−0.24	− 0.53*	−0.33							
Chl a	0.41*	0.19	0.73***	−0.22						
[Bact.]	0.17	0.59**	0.36	− 0.74***	0.47*					
[VLP]	0.03	0.31	0.24	− 0.66**	0.24	0.77***				
BP	0.21	0.75***	0.26	− 0.76***	0.21	0.89***	0.65**			
FVIC	−0.25	−0.27	0.34	0.14	0.61**	0.17	0.06	−0.03		
BS	0.01	0.38	−0.01	−0.34	0.01	0.36	0.36	0.51*	−0.17	
FLC	0.06	0.01	0.50*	−0.18	0.63**	0.25	−0.03	0.12	0.67**	−0.14

potentially high, inductibility with mitomycin is low (Table 2). Elsewhere, Hann Bay is a heavily polluted site, receiving tremendous amounts of untreated toxic industrial and domestic waste, which severely impacts the chemical quality of waters. We know that environmental pollutants can be efficient inducing agents (Cochran et al., 1998). Thus, the combination of high UV radiation and abundant chemical contaminants may reinforce the occurrence of local environmental inductors to elucidate the suspected few mitomycin c-sensitive marine bacteria.

Although the hypothesis of widespread natural inductions has already been formulated on several occasions (Cochran and Paul, 1998; Weinbauer and Suttle, 1999), no data can clearly confirm this presumption. Overall, this scenario is furthermore arguable because of the lack of high-energy, short-wavelength UV radiation (UVC) stopped by the stratospheric ozone layer. An alternative explanation is that viral interactions of either form are not important in this environment, being supplanted by high levels of bacterivory, which invalidates scenario 4 (low predation pressure); however, this parameter was not measured in this study.

In conclusion, at some specific locations, we hypothesize that the physical environment (particularly light), along with the resource availability, may be decisive for phages in favouring one of the two viral life cycles. We suggest that TEM observations of visibly infected bacterial cells considered to be lytically infected may correspond to an unknown extent to recently inducted indigenous lysogenic bacteria. Thus the determination of FVIC and FLC to examine the predominance of one type of cycle versus the other may be source of misinterpretation in some particular aquatic environments.

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