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Viral life strategies in a heavily anthropized tropical lagoon

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Abstract

Ecological traits of aquatic microorganisms have been poorly investigated in tropical latitudes, especially in lagoons, which are often subjected to strong anthropogenic influence, conducive to microbial development. In this study, we examined the abundance of both viral and bacterial communities, as well as their interactions (lytic and lysogenic infections) in the water and sediment of seven main stations of the Ebrié Lagoon (Ivory Coast) with contrasting levels of eutrophication. The highest bacterial and viral concentrations in both planktonic and benthic samples were found in the most eutrophicated stations, where viral lytic infections also exhibited their highest values. Conversely, the highest fractions of inducible lysogens were measured in the most oligotrophic stations, suggesting that these two main viral life strategies are mutually exclusive in this lagoon. Our findings also revealed the importance that nutrients (especially ammonium) play as drivers of the interactions between viruses and their bacterial hosts in tropical lagoons.

Keywords: virus, bacteria, lagoon, eutrophication, lysogeny, ammonium

Introduction

Over the last two decades, much attention has been given to viruses and their multiple ecological and biogeochemical roles in aquatic ecosystems (Suttle 2005). Besides being the most abundant and ubiquitous biological entities (Bergh et al. 1989), viruses also play a fundamental role in shaping the structure and diversity of aquatic microbial food webs, both in water and sediment (Suttle 2007). It is now widely accepted that aquatic viral communities consist mostly of phages (Batinovic et al. 2019), which can control the abundance, activity, and diversity of their bacterial hosts (Weinbauer et al. 2004). The dynamics of aquatic viral and bacterial abundance (BA) are most often closely linked at spatial or temporal scales (Mei and Danovaro 2004, Bettarel et al. 2006, 2011a, Sotomayor-Garcia et al. 2020). Marine phages use two major mechanisms for replication: lysogenic and lytic infections (Williamson et al. 2001, Paul 2008). Lytic strategies result in host lysis and production of new progeny viruses, which are directly released in the ambient water. Conversely, in lysogenic infections, the viral DNA is integrated into the host's genome and replicates together with it in a dormant state while waiting for favorable conditions or events (in particular UV, temperature, and pollutants) to trigger prophage activation, virion production, and host lysis.

Numerous studies have examined virus-bacteria interactions to unravel the factors that influence the occurrence of lytic and lysogenic infections in aquatic systems (Weinbauer et al. 1999, Hewson et al. 2001, Paruch et al. 2019, Sotomayor-Garcia et al. 2020). Phage life strategies have been shown to be governed by physicochemical factors such as salinity (Bettarel et al. 2011b), temperature (Abdulrahman Ashy and Agustí 2020), and solar

radiation (Weinbauer et al. 1999, Bettarel et al. 2011b). Lysogeny is generally favored in environments where bacterial hosts are less abundant and/or live in conditions unfavorable to their growth, whereas lytic infections are usually high in productive ecosystems (Bongiorni et al. 2005, Laybourn-Parry et al. 2007), where bacteria are abundant and physiologically active, sustaining the rapid proliferation of phage parasites according to the "Kill-the-Winner" paradigm (Thingstad and Lignell 1997, Winter et al. 2010). However, this relationship is undoubtedly more complex and is increasingly contested: e.g. by the recent theory of "Piggyback-the-Winner," which postulates that lysogeny could be a dominant strategy in environments where bacterial hosts are present in high concentrations (Knowles et al. 2016).

Yet, most of the research on viral replication cycles in aquatic environments has so far been conducted in temperate or polar latitudes. Only a handful of studies have explored the occurrence of phage lifecycles in tropical waters, where microbial processes are somewhat different due to the high level of solar radiation and high temperatures (Peduzzi and Schiemer 2004, Bettarel et al. 2006, Tsai et al. 2018, Pradeep Ram et al. 2018, Cabral et al. 2017, Chen et al. 2019). Moreover, most of the aquatic ecosystems that have been "virally" investigated are restricted to coastal, estuarine, riverine, or lacustrine waters, with lagoons remaining poorly studied. Lagoon ecosystems are subject to strong hydrological and physicochemical variations, linked to significant exchanges between fresh water (rainfall and fluvial inputs) and marine water (Mahapatro 2013). They are also often bordered by large urban areas, due to the economic resources and services they provide to local populations. These characteristics, added to their

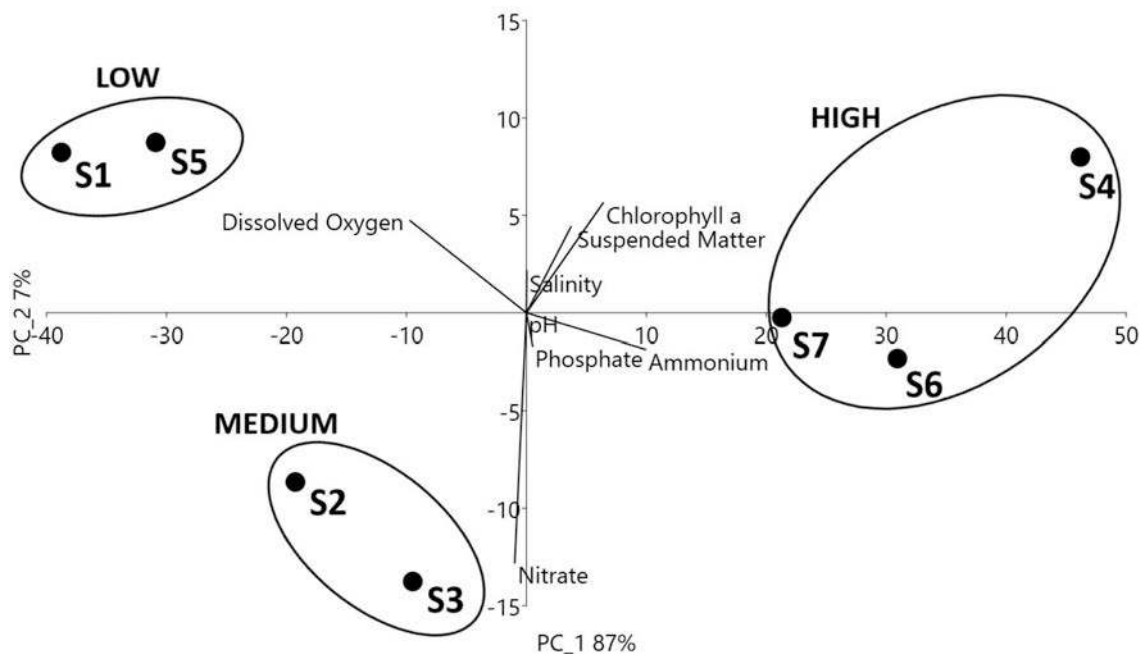


Figure 1. Ordination of the seven stations (S1–S7) by bi-plot graph using the PCA based on physicochemical parameters.

restricted water exchange with the sea, long water residence times, and massive amounts of allochthonous inputs (natural or anthropogenic), make lagoons among the most vulnerable and stressed aquatic ecosystems on Earth (Pérez-Ruzafa et al. 2019).

The case of the Ebrié Lagoon in Ivory Coast, one of the largest lagoons in West Africa, is emblematic (Adingra and Arfi 1998). The lagoon is closely linked to the culture, history, and economic development of the country. It has been affected by the rapid population growth of the capital city of Abidjan, accompanied by intensifying industrial, domestic, and agricultural activities. This has resulted in a high level of eutrophication in Ebrié's waters over the last two decades (Scheren et al. 2004, Yao et al. 2007). The lagoon serves as a receptacle of huge quantities of solid and liquid wastes, often untreated, from bays and rivers around Abidjan (Kouassi et al. 1995, Scheren et al. 2004). These pollutants can interact with environmental factors (chemical and physical), and consequently disrupt microbiological processes in the water column and sediment.

The objective of this study was to investigate the distribution of both viral and bacterial communities and their interactions (lysogenic versus lytic phage lifecycles) in this highly anthropized ecosystem: to our knowledge the first study to examine this in the Ebrié Lagoon. To this end, we sampled different stations around the lagoon with contrasting sources and levels of pollution.

Materials and methods

Study site and sample collection

Samples were collected between 21 and 28 May 2019 in the Ebrié Lagoon, which is surrounded by the city of Abidjan (which has a population of almost 5 million), Ivory Coast's main city. A total of seven different stations were sampled around the lagoon, which had contrasting sources and levels of anthropogenic influence: (S1, 05° 11' 15.8" N, 03° 41' 20.8" W) Mondoukou is the furthest station from the city center, and the least impacted by anthropogenic activities; (S2, 05° 19' 41.1" N, 03° 59' 26.4" W) is a confined site near the French Embassy receiving hospital, agriculture, and urban

discharge; (S3, 05° 18' 26.0" N, 04° 02' 18.0" W) Yopougon Beach is a site with significant fish landing activity and a large marketplace; (S4, 05° 18' 31.1" N, 04° 04' 08.3" W) Pougou Bay is a confined embayment receiving large amounts of untreated urban sewage; (S5, 05° 17' 15.0" N, 04° 01' 48.6" W) Boulay Island is a densely populated fishing village without sanitation facilities; (S6, 05° 15' 58.3" N, 03° 58' 01.1" W) Bietri slaughterhouse is a site that receives animal feces (particularly sheep and cattle) before slaughter; and (S7, 05° 15' 37.0" N, 03° 58' 28.8" W) Bietri Neck is historically Ebrié Lagoon's most confined site, receiving huge quantities of urban discharge (Lanusse 1987, Adingra and Arfi 1998, Kouassi et al. 2009).

Sampling strategy

At each station, both sediment and water samples were sampled. Water samples were collected between a depth of 40 and 50 cm with 1.5 l sterile plastic Nalgene bottles. Sediment samples were collected with a grab sampler (Van Veen). The top layer of the sediment cores (~ 2 cm) was retrieved and placed in sterile zipped plastic bags (Whirl-pak). All samples were kept cool in an icebox during transportation to the laboratory, where they were analyzed within 3 h after collection.

Measurements of physicochemical parameters

During the field sampling, temperature, pH, dissolved oxygen (O₂) concentration, and conductivity of the water samples were determined by using a multiparameter probe (Noetek Ponsel Odeon) that was calibrated just prior to the field campaign. The salinity was calculated from the conductivity and temperature value pairs. Water samples for the measurement of suspended matter (SM) were filtered on preweighed (1/10 mg) Whatman GF/F glass fiber filters (diameter 47 mm; porosity 0.7 μm) previously dried (105°C). After filtration, the filters were dried again (105°C, 2 h) and then reweighed. The SM concentrations were obtained by relating the difference in mass to the filtered volume. Filtrates were frozen (-15°C) immediately after filtration and remained frozen until nutrient analyses were performed. Dissolved inorganic

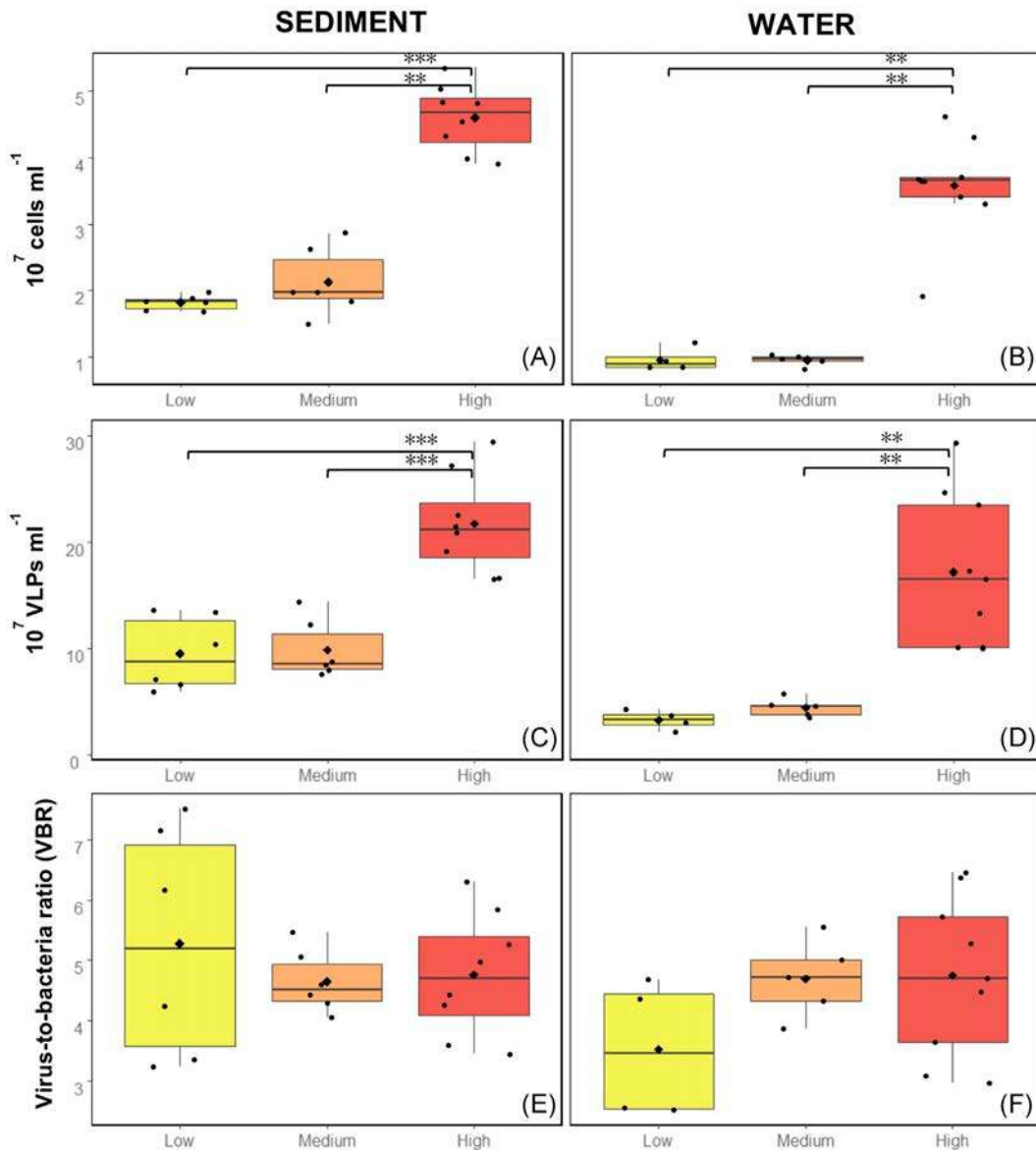


Figure 2. Comparison of the different microbiological traits [(A) and (B): BA, (C) and (D): VA, and (E) and (F): VBR] between the three clusters (i.e. Low, Medium, and High) in sediment and water samples. All the three colored boxplots display the median values (horizontal lines) and quartiles (boxes edges) values in the three clusters. The boxplot whiskers indicate the minimum and maximum values. Each dot in the boxplots represent the value of the microbial traits measured for individual stations and lozenge represents the mean value of the microbial traits for each cluster. Significant differences between the three clusters are represented by ** ($P \leq .01$) and *** ($P \leq .001$). Virus-like particles (VLPs).

nitrogen (ammonium (NH_4) and nitrate (NO_3)) and dissolved reactive phosphorus (PO_4) concentrations were determined by spectrophotometry following the conventional protocols recommended by Aminot and K  rouel (2006). Water samples dedicated to phytoplankton biomass measurements were filtered through Whatman GF/F filters (diameter 25 mm; porosity 0.7 μm). Filters were later grounded in 90% acetone and extracted for 24 h in the dark at 4°C. Chlorophyll *a* (Chl *a*) concentrations were measured by spectrophotometry (Perkin-Elmer LS50b) and calculated following Neveux and Lantoin   (1993).

Enumeration of planktonic and benthic viruses and bacteria

At each station ($n = 7$), triplicate water and sediment samples ($n_{\text{wat}} = 21$; $n_{\text{sed}} = 21$) were distributed into cryotubes (4.5 ml) and fixed with 0.02 μm filtered formaldehyde (final concentration

2% v/v), then flash-frozen in liquid nitrogen and stored at -80°C prior to enumeration of viruses and bacteria. The abundance of planktonic viruses and bacteria was determined from 300 μl of formaldehyde-fixed water samples after retention of particles on 0.02 μm pore-size membranes (Anodisc) and staining with SYBR Gold, as previously described (Patel et al. 2007). Viruses and bacteria were counted with an Olympus AX70 epifluorescence microscope in 20 fields at x100 magnification under blue light excitation (488 nm). Benthic viruses and bacteria were extracted following the recommendation of Danovaro and Middelboe (2010). This involved weighing 1 g of formaldehyde-fixed sediment samples and then resuspending them with 9 ml of distilled water filtered at 0.02 μm . The sediment suspension was homogenized and a pyrophosphate solution was added (5 mM final concentration v/v). The suspension was then incubated for 15 min in the dark. The samples were treated with an ultrasonic processor (Bioblock) at

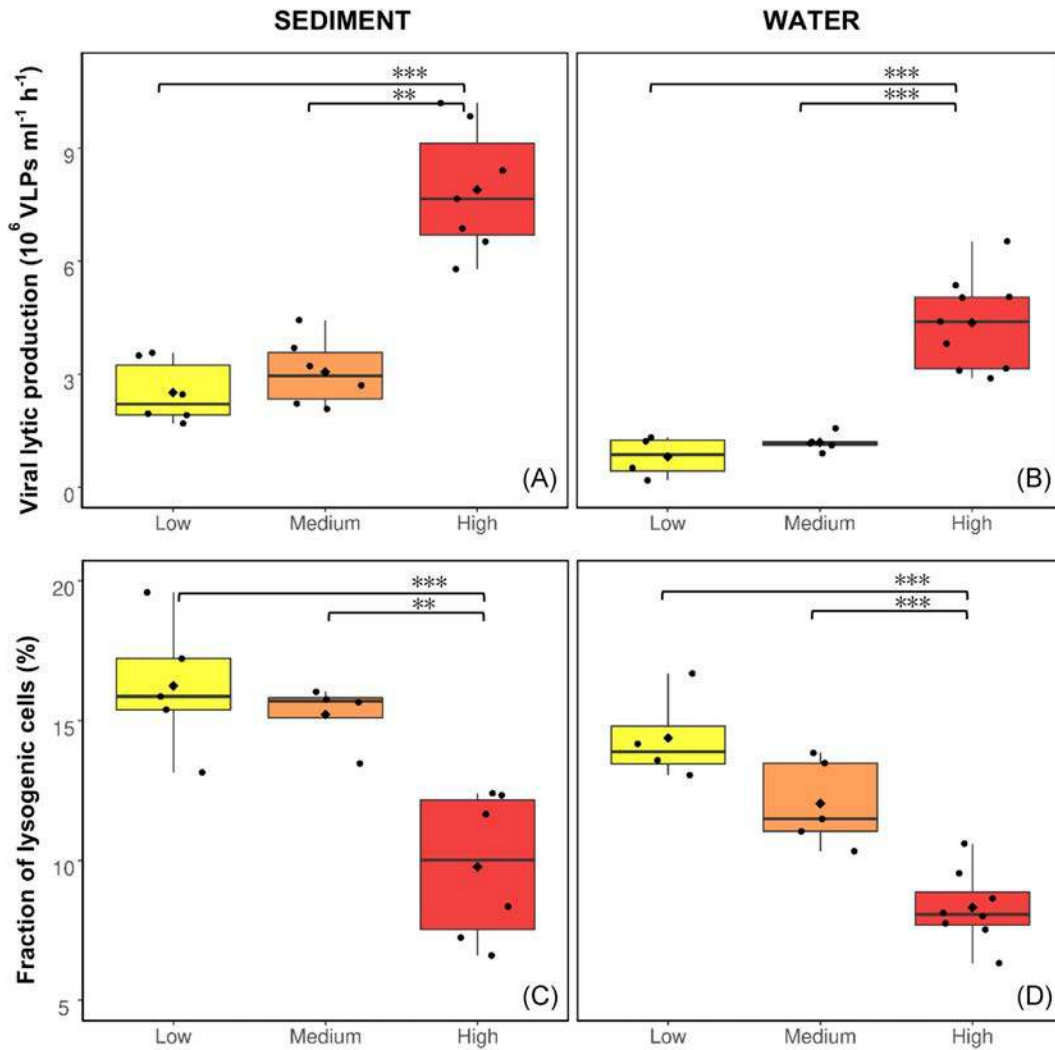


Figure 3. Distribution of the two viral replication cycles [(A) and (B): lytic infections, (C) and (D): lysogenic infections] in the three clusters (i.e. Low, Medium, and High) in sediment and water samples. Each dot in the boxplots represents the value of the fraction of lysogenized cells (FLC) and of VP measured at each station and lozenge represents the mean value of FLC and VP for each cluster. Significant differences between the three clusters are represented by **($P \leq .01$) and ***($P \leq .001$). Virus-like particles (VLPs).

45 KHz amplitude for 3 min (3 cycles of 1 min followed by 30 s of manual shaking) and then centrifuged at 800 g for 15 min. The supernatant was collected, and a volume of 300 μ l was used for the enumeration of viruses and bacteria as described above.

Fraction of lysogenic bacteria

At each station, the fraction of lysogenic bacteria (FLC) was obtained from triplicates of water and sediment ($n_{\text{wat}} = 21$; $n_{\text{sed}} = 21$) by prophage induction using mitomycin-C (Weinbauer et al. 2003). Mitomycin-C (final concentration 1 μ g ml⁻¹, Sigma Aldrich) was added to 3 ml of samples (treated samples). Untreated samples (control incubations) and treated samples with mitomycin C were incubated for 24 h in the dark at *in situ* temperature and were then fixed with 0.02 μ m filtered formaldehyde (final concentration 2% v/v). Viral abundance (VA) in untreated samples and treated samples with mitomycin C was determined using SYBR Gold and epifluorescence microscopy as described above. Phage induction was estimated as the difference between the VA in mitomycin C-treated samples (V_m) and the VA in control samples (V_c). The FLC was calculated as: $\text{FLC} (\%) = [(V_m - V_c)/BS \times BA_{t0}] \times 100$, where BA_{t0} represents the BA before the addition of mitomycin C, and

BS represents the burst size (number of virus particles per bacterium). The chosen value for BS was 24, as this is an average value from previous aquatic environment studies (Wommack and Colwell 2000, Parada et al. 2006).

Viral lytic production

Viral decay, which is the decrease in viral concentration over time, was recorded after inhibition of new viral lytic production (VP) by the addition of potassium cyanide (KCN; final concentration, 5 mM) to 4.5 ml of each triplicate of water and sediment samples ($n_{\text{wat}} = 21$; $n_{\text{sed}} = 21$; Fischer et al. 2004). All incubations for decay experiments were performed at *in situ* temperature for 24 h, in the dark. Incubations were stopped after the addition of 0.02 μ m filtered formaldehyde (final concentration 2% v/v). The sediment samples were further treated to desorb viruses, based on extraction with a pyrophosphate solution followed by sonication (see details in the above section *Enumeration of planktonic and benthic viruses and bacteria*) VA was determined in KCN-treated and KCN-untreated water and sediment samples using SYBR Gold and epifluorescence microscopy (see above). The difference between the

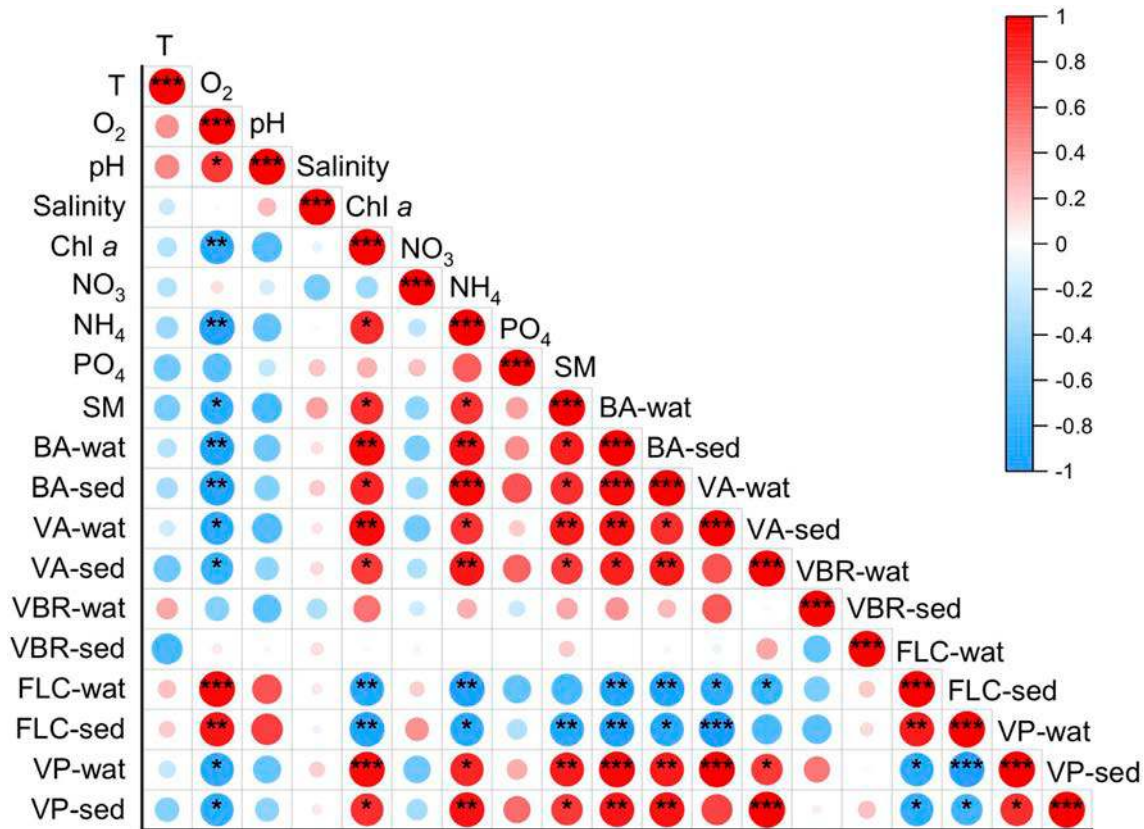


Figure 4. Pearson correlations between environmental parameters and microbial traits in water (wat) and sediment (sed) samples. Temperature (T), dissolved oxygen (O_2), pH, salinity, Chl *a*, NO_3 , NH_4 , phosphate (PO_4), SM, BA, VA, VBR, fraction of lysogenic cells (FLC), and Viral Production (VP). Red and blue circles indicate a positive and negative value, respectively. Significant P-values for Pearson's correlation coefficients are represented by * ($P \leq .05$), ** ($P \leq .01$), and *** ($P \leq .001$).

abundance of viruses with and without KCN allows the estimation of VP (Heldal and Bratbak 1991).

Statistical analyses

The ordination and hierarchical clustering of the seven stations (S1–S7) by bi-plot graph [using a principal component analysis (PCA)] based on physicochemical parameters, and the correlation between all datasets (using a nonparametric Pearson's correlation test), were performed with the software PAST "PALaeontological STatistics" (Dieumegard 2007). Using R software, viral and bacterial abundances, VBR, the fraction of lysogenic bacteria, and the VP rate were compared between the resulting clusters with the nonparametric Kruskal–Wallis and Anova test. Statistical significance was assumed when $P \leq .05$.

Results and discussion

To assess the level of anthropogenic influence in the seven sampling stations of the Ebríe Lagoon, the ordination and clustering of the stations were performed based on the dissolved oxygen rate (O_2), nutrient concentration (NH_4 and NO_3), SM, and Chl *a* concentration, with the two principal components PC_1 and PC_2 (Figs 1 and 2; Table 1). A total of three different clusters were clearly observed, following a clear level of eutrophication: "LOW" (in sites S1 and S5) exhibited a high dissolved oxygen rate, low nutrient concentration, low SM, and low Chl *a* concentration; "MEDIUM" (in sites S2 and S3) was moderately oxygenated, with high NO_3 concentration, low SM, and low Chl *a* concentration; and "HIGH"

(in sites S4, S6, and S7), which were the least oxygenated sites with the highest NH_4 concentration, SM, and Chl *a* concentration (Fig. 1).

The bacterial and viral abundances (benthic and planktonic) obtained in this study were within the same range (10^7 – 10^9 cells and VLPs ml^{-1}) as those usually reported in tropical waters, where high temperatures stimulate bacterial growth, promoting the production of their phage parasites (Pradeep Ram et al. 2018, Bettarel et al. 2006, Parikka et al. 2017, Yucel-Gier et al. 2018; see Fig. 2). On average, viral and bacterial concentrations were significantly higher in the benthic than planktonic samples (Wilcoxon test, $P \leq .01$). Marine sediments, by providing virus and bacteria with excellent preservation and reproduction conditions (Mei and Danovaro 2004, Bettarel et al. 2006, Rastelli et al. 2019), have been identified as microbial hotspots harboring highly diversified and abundant prokaryotic and viral communities (Hewson et al. 2001, Filippini and Middelboe 2007, Danovaro et al. 2008, Quero et al. 2015). Since sediment represents a confined compartment with reduced distance between bacteria and phages, the probability of contact between them is typically high (Danovaro et al. 2008), and this may affect the viral lysis rate and enhance viral proliferation and accumulation.

VBR, which is sometimes used a proxy of virus–bacteria interactions, did not vary significantly between the planktonic and benthic compartments, nor between the three clusters (Fig. 2E and F). The VBR ranged between 3.4 and 6.3 in the water samples (mean_{wat} = 4.4 ± 1.0) and between 3.6 and 6.9 in the sediment (mean_{sed} = 4.9 ± 1.2). Similar values were found in a study

Table 1. Physicochemical values measured in the water samples of the seven sampling stations (S1–S7). Temperature (T), dissolved oxygen (O₂), Chl *a*, NO₃, NH₄, phosphate (PO₄), and SM.

Station	Cluster	T (°C)	O ₂ (%)	pH	Salinity	Chl <i>a</i> (μg l ⁻¹)	NO ₃ (μM)	NH ₄ (μM)	PO ₄ (μM)	SM (mg l ⁻¹)
S1	LOW	31.4	78.0	7.5	14.1	3.5	0.4	4.4	0.1	16.9
S5		29.2	72.0	7.3	15.9	11.5	5.4	2.2	0.8	27.9
S2	MEDIUM	30.2	58.2	7.2	8.4	17.7	18.4	8.6	1.4	16.9
S3		29.4	52.2	7.1	13.8	5.7	19.1	22.4	3.5	26.4
S4	HIGH	29.9	23.0	6.9	13.2	43.6	0.0	50.0	1.5	42.6
S6		29.3	35.5	7.2	12.5	29.7	6.6	51.7	4.0	31.3
S7		29.7	34.1	7.2	16.3	27.0	5.3	36.3	5.1	32.0

conducted in tropical freshwater sites located in the basin of the Senegal River (Bettarel et al. 2006). However, contrary to our results, the authors observed that VBR was significantly higher in the water column than in the sediment. The existence of a relationship between RBV and the trophic level of aquatic ecosystems also remains unclear. Indeed, (Maranger and Bird 1995) found no correlation between the VBR and the trophic status of 22 lakes in Quebec lakes. Conversely, Bettarel et al. (2004) proposed that VBR increase together with the lake productivity. Finally, the lack of clear pattern and the relatively high variability in the VBR values may be explained by the burst size and infection rate of bacteria cells, which are also highly variable among ecosystems (Wommack and Colwell 2000, Hewson et al. 2001). Due to contradictory results, trends in VBR have led to misinterpretation (Parikka et al. 2017) and according to our result, VBR values were not satisfying to explain interactions between viral and bacterial communities and their link with the levels of eutrophication.

One of the study's main findings was that bacterial and VA, as well as phage lytic production, were all significantly higher in the most eutrophicated cluster (HIGH) than in the two other less productive clusters (MEDIUM and LOW), regardless of the compartment (water and sediment; see Figs 2 and 3). Interestingly, all these parameters were positively and significantly correlated with NH₄ and Chl *a* concentrations (Pearson correlation, $P \leq .05$, Fig. 4). Nutrient-rich environments typically act as fertilizers promoting phytoplankton growth, which contributes greatly to the utilizable dissolved organic material required to supply bacterial growth (Kritzberg et al. 2006, Pringault et al. 2020). Furthermore, inorganic nutrients are essential for the growth of bacterial phage hosts (Wilson and Mann 1997, Freese et al. 2007); we know that the ability of viruses to replicate is directly influenced by the physiological state of their host, with lytic viral infections favored by metabolically active hosts (Weinbauer 2004, Parada et al. 2006). Given the large demand for nitrogen and phosphorus during viral replication processes (Jover et al. 2014), it is not surprising to observe the highest levels of VP and concentration in the stations with the most eutrophication.

Conversely, the fraction of lysogenic cells (FLC) was significantly lower in the most eutrophicated cluster (Fig. 3). Such results are in line with previous findings showing that lysogeny is a dominant reproduction pathway in low productive environments, where the abundance of potential hosts is reduced (Williamson et al. 2001, Weinbauer et al. 2003, Paul 2008, Bettarel et al. 2011b, Maurice et al. 2010, Brum et al. 2016). However, since the “Piggyback-the-Winner” hypothesis was put forward (Knowles et al. 2016), recent findings have strongly questioned this view. That model, developed essentially from data obtained on animal microbiomes, suggests that lysogeny could also be a relevant strategy at high bacterial host density, by providing many ecological benefits to infected bacterial communities, in particular by

allowing them to escape the lytic pressure of phages and conferring superinfection exclusion, and thus continue to fulfill their functions (defence and nutrition) for the host (Silveira and Rohwer 2016, Howard-Varona et al. 2017, Silveira, Luque and Rohwer 2021).

Finally, our results indicated that the specific environmental context of the study site (i.e. a tropical lagoon with high temperatures and high eutrophication) seemed favorable to the development of virulent rather than temperate viruses. Overall, given the numerous but relatively contradictory data reported in the literature, our study suggests that the conditions favoring lysogeny or lytic strategies remain highly ambiguous and would benefit from further investigation, especially along larger latitudinal and eutrophication level.

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Conflict of interest. None declared.

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