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## Pelagic food web patterns: do they modulate virus and nanoflagellate effects on picoplankton during the phytoplankton spring bloom?

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4 **Pelagic food web patterns: do they modulate virus and nanoflagellate effects on**  
5 **picoplankton during the phytoplankton spring bloom?**  
6

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24  
25 **Running title:**

26 Effects of viruses and nanoflagellates on picoplankton

## 27 **Summary**

28 As agents of mortality, viruses and nanoflagellates impact on picoplankton populations. We  
29 examined the differences in interactions between these compartments in two French Atlantic bays.  
30 Microbes, considered here as central actors of the planktonic food web, were first monitored  
31 seasonally in Arcachon (2005) and Marennes-Oléron (2006) bays. Their dynamics were evaluated  
32 to categorize trophic periods using the models of Legendre and Rassoulzadegan (1995) as a  
33 reference framework. Microbial interactions were then compared through 48h-batch-culture  
34 experiments performed during the phytoplankton spring bloom, identified as herbivorous in  
35 Marennes and multivorous in Arcachon. Marennes was spatially homogeneous compared to  
36 Arcachon. The former was potentially more productive, featuring a large number of heterotrophic  
37 pathways, while autotrophic mechanisms dominated in Arcachon. A link was found between  
38 viruses and phytoplankton in Marennes, suggesting a role of virus in the regulation of autotroph  
39 biomass. Moreover, the virus-bacteria relation was weaker in Marennes, with a bacterial lysis  
40 potential of 2.6% compared with 39% in Arcachon. The batch experiments (based on size-  
41 fractionation and viral enrichment) revealed different microbial interactions that corresponded to  
42 the spring-bloom trophic interactions in each bay. In Arcachon, where there is a multivorous web,  
43 flagellate predation and viral lysis acted in an opposite way on picophytoplankton. When together  
44 they both reduced viral production. Conversely, in Marennes (herbivorous web), flagellates and  
45 viruses together increased viral production. Differences in the composition of the bacterial  
46 community composition explained the combined flagellate-virus effects on viral production in the  
47 two bays.

48

## 49 **Introduction**

50 The long held paradigm that primary production is transferred through a herbivorous chain to small  
51 and large phytovores neglects the importance of most microorganisms. Yet bacteria, which are  
52 present at up to  $10^6$  cells.ml<sup>-1</sup>, and viruses, whose concentration can reach  $10^8$  viral particles.ml<sup>-1</sup>,

53 dominate in the oceans (Borsheim et al., 1990; Hennes and Suttle, 1995; Li, 1998). Bacteria were  
54 primarily considered as remineralizers providing inorganic nutrients for primary producers. Later,  
55 the microbial loop concept (Azam et al., 1983) highlighted the role of bacteria as recyclers of DOM  
56 originating either from primary production or from losses at different trophic levels. Thus, the role  
57 of bacteria in the microbial loop evolved from that of a matter sink to a trophic link towards  
58 bacterivorous organisms. Moreover, bacterial community dynamics are not only controlled by  
59 resources i.e. bottom-up control, such as the availability of inorganic nutrients and the quality of  
60 DOM (Kirchman et al., 2000), but also by predation i.e. top-down control, examples being the  
61 mortality induced by protists such as nanoflagellates and ciliates and by viral lysis. (Sanders et al.,  
62 1992; Fuhrman, 1999). The selectivity of protist predation based on size, motility, shape and cell  
63 surface properties of prey (Gonzalez et al., 1990; Monger et al., 1999) can potentially impact on the  
64 morphological characteristics of bacteria and shape their community composition (BCC) (Hahn and  
65 Hofle, 2001; Posch et al., 2001). On an ecosystem level, protist predation may exert a stronger  
66 control in oligotrophic waters than in eutrophic waters (Gasol et al., 2002).

67 Since the 1990's, viruses have been considered as an additional factor in the mortality of bacteria  
68 (Fuhrman, 1999), other micro-organisms such as microalgae (Cottrell and Suttle, 1995) and  
69 unpigmented flagellates (Garza and Suttle, 1995; Massana et al., 2007). Virus-mediated bacterial  
70 mortality could account for 48-84% of bacterial production in oligotrophic areas and 59% in  
71 eutrophic areas (Boras et al., 2009). Regarding the biogeochemical aspects of the ecosystem, viral  
72 lysis shunts carbon flow (Fuhrman, 1999): 6 to 26% of photosynthetically fixed carbon flows back  
73 to DOM, becoming available for microbial uptake and consequently modifying the competitive  
74 balance of phytoplankton and bacteria for limiting nutrients (Wilhelm and Suttle, 1999). Moreover,  
75 viral infection could potentially maintain the species richness of bacteria, as described in the "kill  
76 the winner" concept (Thingstad and Lignell, 1997). The density dependence of viral infection could  
77 limit dominant and competitive bacteria and give an advantage to less competitive ones (Bouvier  
78 and Del Giorgio, 2007; Weinbauer et al., 2007; Auguet et al., 2009), although this idea is still

79 controversial (Winter et al., 2004). In addition, host specificity could concern strains instead of  
80 species because of the phenotype plasticity of the viral permissivity-resistance characters  
81 (Schwalbach et al., 2004; Fuhrman, 2009).

82 Even if virioplankton is mainly composed of bacteriophages (Fuhrman, 1999; Suttle, 2005), a link  
83 with phytoplankton or chlorophyll *a* concentrations, suggesting phytophage pathogenicity  
84 (Wommack and Colwell, 2000), has already been underlined in some long term surveys where there  
85 were high densities of algal cells (Maranger et al., 1994) as well as in offshore stations (Boehme et  
86 al., 1993; Guixa-Boixereu et al., 1999) or in coastal regions at the deep chlorophyll *a* maximum  
87 (Baudoux et al., 2008). Organisms less than 3 $\mu$ m in size may be responsible of large part of primary  
88 production, in particular in oligotrophic areas (Platt et al., 1983). Autotrophic as well as  
89 heterotrophic pico- and nanoplankton are too small to be efficiently consumed by metazoans (Sherr  
90 and Sherr, 1988); they are mainly consumed by flagellates and ciliates (Sherr and Sherr, 1994) and  
91 can significantly contribute to their diet (Hirose et al., 2008). However, the grazing yield from  
92 phytoplankton is lower than from bacteria. Furthermore, predation on protists indirectly affects  
93 bacterial grazing, enhancing viral impact (Boras et al., 2009). Thus, as the preferential prey of  
94 copepods (Nielsen and Kiorboe, 1994), ciliates can be considered as a trophic link between pico-  
95 and nano-plankton and mesozooplankton (superior trophic levels) (Calbet and Saiz, 2005).

96 To assess the importance of microbiological plankton compartments in matter flow, Legendre and  
97 Rassoulzadegan (1995) described 4 major trophic concepts each incorporating different dominant  
98 carbon pathways: (1) The herbivorous or classical food web, which is based on large-phytoplankton  
99 (>5 $\mu$ m) primary production leading to large zooplankton organisms. (2) The microbial food web, in  
100 which primary production is mainly due to small phytoplankton and comprises pathways involving  
101 heterotrophic bacteria and protozoa. (3) The microbial loop, a nearly closed system where carbon  
102 flows are limited to heterotrophic bacteria and unpigmented protists; DOM released by the grazers  
103 becomes substrate for bacteria. (4) Finally, the multivorous food web, a transitional trophic system

104 comprising diverse heterotrophic carbon pathways in which both large and small phytoplankters are  
105 significant primary producers.

106 Accordingly, the question arises: do the interactions between microbial compartments (in particular  
107 between viruses, picoplankton and nanoflagellates) vary depending on the trophic pathway? So far,  
108 despite the clear importance of heterotrophic microorganisms in pelagic food webs, descriptions of  
109 trophic models have mostly been based on primary producer size, water column stratification and  
110 nutrients (Rivkin et al., 1996; Marquis et al., 2007). Thus, to answer this question, two sites along  
111 the French Atlantic coast that are distinctive in terms of their river inputs and hydrology (shape,  
112 mixing regime and water residence time) were chosen as study case areas to describe the temporal  
113 succession of trophic pathways. The temporal dynamics of abiotic parameters and microbiological  
114 compartments were assessed over 7 months in Arcachon Bay in 2005 and over one year in  
115 Marennes Oléron Bay in 2006. Located North-Southward along the coast of the Bay of Biscay,  
116 Arcachon and Marennes-Oléron Bays are both semi-enclosed and macrotidal lagoons, largely  
117 composed of intertidal mudflats (Blanchet et al., 2008; Allard et al., 2009). Like many estuaries and  
118 bays, the 2 basins are highly productive, featuring a large-phytoplankton spring bloom (Struski and  
119 Bacher, 2006; Glé et al., 2008). In this context, does the large-phytoplankton spring bloom entail  
120 similar trophic pathways in each bay and thus similar interactions between the above-mentioned  
121 microbial compartments? To answer this question, we first defined the trophic succession for each  
122 bay, then located the spring phytoplankton bloom within this succession, and finally *in vitro*  
123 experiments were performed during this period to analyse the quantitative and qualitative impact of  
124 nanoflagellate grazing and viral lysis on picoplankton.

125

126

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129

## 130 **Results**

### 131 ***IN SITU SURVEYS***

#### 132 *Environmental context*

133 The evolution of the abiotic parameters in the 2 bays followed a typical temperate-coastal pattern  
134 featuring peak temperatures and salinities in the summer together with low nutrient levels during  
135 the period of low runoff. On average, Arcachon Bay (Arc) had fewer nutrients than Marennes (M-O)  
136 (Table S1 and S2). Arc waters were spatially heterogeneous, with significant differences of salinity,  
137 temperature and most nutrients between the 2 stations (ANOVA,  $H_0$  no difference between stations  
138 is rejected,  $p < 0.05$ ). By contrast, M-O was homogeneous over 4 of the 5 stations (ANOVA  $p > 0.05$ ).  
139 The Charente station differed from the four others, with higher nutrient levels and lower salinity  
140 (ANOVA with Tukey multiple comparisons,  $p > 0.05$ ) (Table S1).

141

#### 142 *Zonation and seasonality of microbial distribution*

143 The bacteria/virus relationship ( $r^2 \geq 0.6$ ) in Arc was stronger than in M-O. However, the response of  
144 bacteria to increasing viruses was weaker in Arc (log/log regression slopes  $\leq 0.6$ ) than in M-O  
145 (slopes  $\geq 0.84$ , Table 1). In Arc, bacterial (BA) and viral (VA) abundances in Comprian were  
146 significantly higher than in B13 (ANOVA,  $p < 0.0002$ , Table 1). In M-O, the BA/VA relationship  
147 was equal in 4 of the 5 stations (Slope comparison, ANCOVA,  $p < 0.05$ ,  $n=96$ ), but the relationship  
148 was insignificant at Charente station ( $p=0.09$ ) (Table 1). Nevertheless, no significant differences in  
149 the annual abundance of viruses and bacteria were found between the 5 stations (ANOVA,  $p < 0.05$ ).  
150 Consequently, the global monthly and annual means (BA:  $4.11 \pm 0.34 \times 10^6$  cells.ml<sup>-1</sup> and VA:  
151  $3.38 \pm 0.34 \times 10^7$  particles.ml<sup>-1</sup>) are representative for the whole basin. The VBR (virus to bacteria  
152 ratio) was higher in M-O (annual mean =  $11.16 \pm 5.39$ ) compared to Arc ( $4.06 \pm 1.17$  and  $4.89 \pm$   
153  $1.96$  at B13 and Comprian, respectively). In M-O, VBR tended to be higher from November to  
154 April ( $>10$ ) and lower during summer ( $<10$ ), while no trend was visible in Arc (data not shown).

155 The results of PCA and HAC were analysed to compare the spatial and temporal organization of the  
156 2 bays (Fig. 1). Only samples from January to August were taken into account. Nutrients (23%) and  
157 viruses (7.5%) contributed positively to axis 1 while Cryptophyceae (10%), salinity (5%), diatoms  
158 (5%) and *Synechococcus* (5%) contributed negatively. Small phytoeukaryotes (16%), temperature  
159 (14%), bacteria (12.5%) and ciliates (12.5%) contributed positively to axis 2. The 2 axes accounted  
160 for 52.67% of the total variance among the samples. Along the first axis, Arc was distinguished  
161 from M-O by low nutrients (Table S1), a high abundance of autotrophs [Diatoms (mean:  
162  $3.52 \pm 4.17 \times 10^5 \text{ cell.l}^{-1}$  vs.  $0.65 \pm 1.45 \times 10^5 \text{ cell.l}^{-1}$ ), Cyanobacteria (mean:  $1.77 \pm 2.83 \times 10^4$  vs.  
163  $3.9 \pm 2.9 \times 10^3 \text{ cell.ml}^{-1}$ ), Cryptophyceae ( $6.46 \pm 5.17 \times 10^4$  vs.  $13 \pm 28 \text{ cell.l}^{-1}$ )], as well as low VA  
164 ( $5.71 \pm 5.23 \times 10^6$  vs.  $3.37 \pm 1.21 \times 10^7 \text{ particles.ml}^{-1}$ ). Seasonal clusters were found along the second  
165 axis for both basins (“winter”: January - April and “summer”: May - August), principally due to  
166 higher summer temperatures combined with a higher abundance of microorganism in Arc (bacteria,  
167 ciliates and pico- nanophytoplankton). Furthermore, a spatial subdivision appeared in Arc along  
168 axis 1, distinguishing the inner (Comprian) from the outer (B13) sampling station. By contrast, the  
169 M-O stations were homogeneous, although the Charente station points were always shifted to the  
170 right because of a lower salinity and a higher level of nutrients. Moreover, the Charente station was  
171 also distinguished by large amounts of suspended matter (Table S1).

172 Based on the results of this multivariate assessment, the basin dynamics were further distinguished  
173 using the inner station of Arc (Comprian) and averages of the five M-O stations (because of their  
174 spatial homogeneity) using multiple regressions. VA and BA dynamics can be related to the more  
175 complex relationships in M-O compared to Arc (Table 2). The opposite was observed for  
176 heterotrophic nanoflagellates. There are several important details: (i) in winter, BA was positively  
177 related to viruses in both bays and to HNF in M-O but negatively in Arc. In summer, only the link  
178 with viruses remained along with supplementary links with nutrients (ammonium, nitrite and  
179 phosphate); (ii) there was a negative relationship between viruses and picophytoplankton all year  
180 long in both bays as well as with HNF in Arc during the summer; viruses were positively linked to



181 chla all year round in M-O but not in Arc. (iii) HNF were negatively related to ciliates during winter  
182 (Table 2).

183

#### 184 *Temporal succession of trophic pathways*

185 Herbivorous food webs were identified for 20% of the sampling period in Arc (February and  
186 August) and for 27% of the period in M-O (May and July-August, Fig. 2A,B). Multivorous webs  
187 were present for 21% of the period in Arc (May and the second half of August) and for 25% of the  
188 period in M-O (3 weeks in February-March and 2 months between mid-October and mid-  
189 December). The microbial food web represented about half of the sampling period in both bays, yet  
190 they were not synchronized, except during March-April (Fig. 2). Finally, the microbial loop was  
191 absent in Arc, while it was present for 5% of the period in M-O (two weeks at the end of March and  
192 one in September). During these two periods, bacteria grew 2.0x and 2.4x, viruses 2.0x and 2.0x,  
193 nanoflagellates 6.7x and 1.5x and ciliates 0 and 20x, respectively (Fig. 2B, “Microbial loop”).

194 BA and VA evolved in parallel during all the trophic periods in Arc. However, the synchronisation  
195 was less obvious in M-O, particularly during the herbivorous and multivorous phases when VA did  
196 not decrease as much (-1.6x) as BA (-2.1x).

197 In Arc, the small phytoplankton (annual mean =  $3.4 \pm 1.5 \times 10^4$  cells.ml<sup>-1</sup>) were dominated by  
198 picoplankton, with 3 major growth periods (early April, early May accompanied by nanoplankton,  
199 and from mid-June to end of July, also accompanied by nanoplankton). Large-phytoplankton, with  
200 an annual mean of  $4.73 \pm 4.16 \times 10^5$  cells.l<sup>-1</sup>, dominated at the beginning of the year, with mainly  
201 dinophyceae and cryptophyceae species; this was followed later by two diatom peaks (mid-May and  
202 late August). Three periods of growth of small phytoplankton were observed in M-O (annual mean  
203 =  $1.98 \pm 1.71 \times 10^4$  cell.ml<sup>-1</sup>) that were mostly due to picoplankton (end of April,  $4.9 \times 10^4$  cells.ml<sup>-1</sup>,  
204 early June,  $6.8 \times 10^4$  cells.ml<sup>-1</sup> and early July,  $4 \times 10^4$  cells.ml<sup>-1</sup>). Large-phytoplankton (annual  
205 mean =  $7.05 \pm 14.6 \times 10^4$  cells.l<sup>-1</sup>) developed at the end of March (mainly diatoms), early May (mainly  
206 diatoms) and early July (diatoms and dinoflagellates). Moreover, picophytoplankton and large

207 phytoplankton accounted for the viral dynamics during the herbivorous and multivorous periods in  
208 M-O (simple regression,  $p=0.01$  and  $p=0.006$ , respectively).

209 Nanoflagellate numbers increased systematically during the microbial phases in both Arc and M-O  
210 at the beginning of the herbivorous and multivorous periods, just before the large-phytoplankton  
211 blooms. Small cells dominated in the latter (annual mean:  $88.2\pm 6.9\%$   $<3\mu\text{m}$  cells, Fig. 2). In Arc,  
212 the pigmented/unpigmented ratio of nanoflagellates was higher (mean=11.6 vs. 3.9 in M-O).

213 Ciliate dynamics followed those of bacteria in M-O except in mid-February (Fig. 2B).  
214 Heterotrophic species dominated (annual mean of *Strombidium spp* plus *Strobilidium spp*: 55% and  
215 48% of the total abundance, respectively). The only exception was during the spring phytoplankton  
216 bloom when autotrophic and potentially autotrophic taxa (*Myrionecta rubra*, *Tontonia spp*, *Laboea*  
217 *sp*) represented 60% and 80% of the total abundance. In Arc, ciliate dynamics followed those of  
218 nanoflagellates, increasing during the microbial food web periods.

219 Finally, beyond the fact that the changes in the trophic pathways in the two bays are not  
220 synchronized, the major difference was the contrasting organization at the beginning of the year,  
221 which was herbivorous in Arc and microbial in M-O. Moreover, during the large-phytoplankton  
222 spring blooms, M-O featured a herbivorous web pathway while Arc was in a multivorous phase.

223

## 224 ***IN VITRO* EXPERIMENTS**

225 Experiments were performed with water from Arcachon-Comprian (2006;  $T^{\circ}\text{in situ}= 18.6^{\circ}\text{C}$ ;  $S= 32$   
226 PSU) and the Marennes-Station E (2007;  $T^{\circ}\text{in situ}= 15^{\circ}\text{C}$ ;  $S= 32.5$  PSU) collected at morning high  
227 tide. During incubation, the nighttime/daytime water temperature varied from  $19.5^{\circ}\text{C}$  to  $23.3^{\circ}\text{C}$  in  
228 Arc and from  $18^{\circ}\text{C}$  to  $22^{\circ}\text{C}$  in M-O, respectively.

229

### 230 *Protists*

231 In Arc, the abundance of picophytoeukaryote (picoeuk) was equivalent in all treatments at the  
232 beginning of the experiment ( $1.8\times 10^3$  cells.ml<sup>-1</sup>). In the absence of predators, virus enrichment had a

233 positive effect from 18h to 38h, during which picoeuk abundance increased 18-fold (Fig. 3A). But  
234 in the presence of flagellates, picoeuk abundance dropped 4.5-fold. In M-O water, the abundance of  
235 picoeuk was not significantly different between treatments despite an initial difference due to the  
236 filtration step.

237 Pigmented nanoflagellates were few and varied little in both sites, (means:  $6.4 \times 10^4$  cells.l<sup>-1</sup> in Arc  
238 and  $9.6 \times 10^4$  cells.l<sup>-1</sup> in M-O), making up <1% and <10% of the total nanoflagellates, respectively.  
239 The nanoflagellates started growing at 18h (Fig. 3E). Their growth rates were 2- to 4-fold higher in  
240 Arc than in M-O (in 3 $\mu$ -Tr and 20 $\mu$ -Tr respectively). Moreover, in both bays, the nanoflagellates in  
241 the latter were significantly higher than in 3 $\mu$ -Tr (2way-ANOVA p<0.01) while the small cells  
242 (<3 $\mu$ m) dominated and grew more rapidly than the large ones. During the 48h incubations, the  
243 small/large flagellate ratio increased from 5 to 100 in Arc and from 1.5 to 20 in M-O.

244

#### 245 *Bacterial abundance and growth rate*

246 During the different treatments, bacterial abundance after 48h increased 20-35 fold in Arc  
247 (stationary phase) and 20-60 fold in M-O (logarithmic phase) (Fig. 3B). In Arc, the net bacterial  
248 abundance increase (NBI) was always significantly greater in virus enriched treatments (p=0.005).  
249 In M-O, the viral enrichment enhanced BA only in the 0.8 $\mu$ m treatments (p<0.05).

250 The maximum specific bacterial growth rate ( $\mu_{max}$ ) showed significant differences between  
251 treatments:  $\mu_{max}$  was significantly higher in both bays with virus-enriched treatments compared to  
252 the corresponding controls (2way ANOVA, p=0.02) (cf Fig. 3B black versus clear symbols). The  
253 growth stimulation was 9-14% in Arc and 12-33% in M-O. However, the presence of flagellates did  
254 not significantly modify  $\mu_{max}$  in either of the bays (20 $\mu$ m and 3 $\mu$ m treatments versus 0.8 $\mu$ m  
255 treatments; Fig. 3B)

256 In Arc, during the exponential phase, the growth rate of population 6 of HNA cells, which were the  
257 most abundant, was stimulated in enriched-0.8 $\mu$ -Tr (+44%) compared to the control, while  
258 populations 3, 4 and 5 were inhibited. The presence of flagellates (3 $\mu$  and 20 $\mu$  treatments) masked

259 this particularity. In M-O, the growth rate of population 3 in the presence of flagellates was  
260 significantly higher than those of the other populations (data not shown).

261

### 262 *Viral abundance and production*

263 The initial viral abundance was multiplied 2-3-fold in enriched-treatments in both Arc and M-O  
264 (Fig. 3C). In Arc, some viruses were produced during the first 12 hours, except in 20 $\mu$ -Tr. A second,  
265 stronger production phase was observed between 24 and 38h in all treatments, persisting till the end  
266 of the experiment in 3 $\mu$ -Tr. The presence of flagellates significantly decreased the total viral  
267 production rate (-50% in 3 $\mu$ -Tr and -75% in 20 $\mu$ -Tr) from 0.04 h<sup>-1</sup> in 0.8 $\mu$ -Tr to 0.02 h<sup>-1</sup> in 3 $\mu$ -Tr  
268 and to 0.01 h<sup>-1</sup> in 20 $\mu$ -Tr (2way-ANOVA, p=0.0002). Moreover, viral enrichment decreased the  
269 viral production rate notably in presence of small predators (-47.5%, p=0.009) and in their absence,  
270 yet not significantly (-23%; p=0.1). In M-O, VA evolved differently with the various treatments:  
271 viruses were produced between 12 and 18h only in the presence of flagellates (3 $\mu$ - and 20 $\mu$ -  
272 treatments). There was a second production phase from 38h in all treatments except in the enriched-  
273 0.8 $\mu$ -Tr and 20 $\mu$ -Tr. The net viral production over 48h was negative (-31%, -72%, -5.3%, -70% and  
274 -65% in 0.8 $\mu$ -Tr, enriched-0.8 $\mu$ -Tr, 3 $\mu$ -Tr, 20 $\mu$ -Tr and enriched-20 $\mu$ -Tr respectively) except in  
275 enriched-3 $\mu$ -Tr (+5.8%). In contrast to Arc, a combination of the presence of flagellates and virus  
276 enrichment increased 2.5-fold the total viral production rate (from 0.01 h<sup>-1</sup> in 0.8 $\mu$ -Tr to 0.025 h<sup>-1</sup> in  
277 enriched-3 $\mu$ -Tr). The addition of viruses alone had the opposite effect (2way-ANOVA, interaction,  
278 p=0.006), inducing a significant 6.5-fold decrease (from 0.01 h<sup>-1</sup> in 0.8 $\mu$ -Tr to 0.0016 h<sup>-1</sup> in  
279 enriched-0.8 $\mu$ -Tr).

280

### 281 *Virus mediated bacteriolysis*

282 In Arc, we calculated that 70 $\pm$ 15% of the bacterial stock was lysed per day (0.8 $\mu$ -Tr). In the  
283 presence of flagellates, this impact decreased significantly to 33.7 $\pm$ 1.9% (3 $\mu$ -Tr) and 39 $\pm$ 11% (20 $\mu$ -  
284 Tr) (ANOVA: p=0.01). By contrast, virus mediated lysis was less severe in M-O (13.6 $\pm$ 1.7% of

285 bacterial stock lysed per day without any predators). Small flagellates had no effect ( $9.4\pm 4.6\%$  in  
286  $3\mu\text{-Tr}$ ,  $p>0.05$ ). However, in the presence of all the flagellates ( $20\mu\text{-Tr}$ ), the percentage of lysed  
287 bacteria significantly decreased to  $2.6\pm 0.3\%$  (ANOVA,  $p=0.009$ ).

288

### 289 *Bacterial enzymatic activity and community composition*

290 In Arc, the change in specific maximum velocity of potential aminopeptidase activity (specific  
291  $V_{\max}$ ) was similar in all treatments, with a peak at 24h. Specific activity dropped at 38h except in  
292  $3\mu\text{-Tr}$ , where a strong activity was maintained until the end of the experiment (Fig. 3D). There was  
293 a negative relationship between picoeuk abundance and bacterial proteolytic activity, which was  
294 significant only in the presence of flagellates (Simple regression:  $r^2=92\%$   $p<0.0001$   $n=15$  in  $3\mu\text{-Tr}$ ,  
295  $r^2=29\%$   $p=0.022$ ,  $n=15$  in enriched- $3\mu\text{-Tr}$ ). The specific  $V_{\max}$  peaked also at 24h in M-O, except in  
296 the enriched- $3\mu\text{-Tr}$  at 12h. In both bays, peaks of activity occurred during the exponential growth  
297 phase of bacteria (Fig. 3B, D). Moreover, a decline in bacterial activity coincided with an increase  
298 in viral abundance in both bays: in M-O, there was a negative relationship between VA and specific  
299  $V_{\max}$  in the  $0.8\mu$  and  $3\mu$  treatments ( $\log VA=4.11-0.63 \times \log V_{\max}$ ,  $r^2=0.15$ ,  $n=60$ ,  $p=0.002$ ). This  
300 relationship was still significant ( $r^2=0.13$ ,  $p=0.007$ ) when  $20\mu$  treatments were taken into account.

301

302 At the beginning of the incubations, the *Eubacteria* were less FISH-targeted in Arc (53% of  
303 DAPI stained bacteria in  $0.8\mu\text{-Tr}$  and 35% in  $3\mu\text{-Tr}$ ) than in M-O (62% in  $0.8\mu\text{-Tr}$  and 81% in  $3\mu\text{-Tr}$ ).  
304 In Arc, the dominance of *γ-proteobacteria* (Gamma) was further increased in the presence of  
305 small nanoflagellates (15% versus 8%), while *α-* and *β-proteobacteria* (Alpha and Beta) were  
306 present in relatively similar proportions (2-2.5%) (Fig. 4). In M-O, Gamma were more numerous in  
307 the  $0.8\mu$  treatments (8.9%) than in the  $3\mu$  treatments (3%), while among the other groups, only Beta  
308 in  $0.8\mu\text{-Tr}$  showed up significantly (2.6%).

309 Over 48h, the proportion of *Eubacteria* increased in both bays (78-85% in Arc, 83-90% of  
310 total cells in M-O), with a dominance of Gamma. However, while the proportion of Gamma at 48h

311 was higher in Arc in the presence of flagellates ( $70\pm 5.4\%$ ) than in their absence ( $58\pm 3\%$ ),  
312 independent of viral enrichment, Gamma dominated in M-O ( $\approx 80\%$ ) with no difference between  
313 treatments (Fig. 4). Furthermore, at 48h in Arc, a positive effect of viruses was observed on Beta  
314 and Alpha in the presence of flagellates (+38% in enriched-3 $\mu$ -Tr compared to the control 0.8 $\mu$ -Tr),  
315 counterbalancing the negative impact of predators (-65% in 3 $\mu$ -Tr). However, earlier on, at 12h,  
316 Alpha cells were sensitive to virus inputs (-70% and -75% in enriched-0.8 $\mu$ -Tr and enriched-3 $\mu$ -Tr  
317 respectively, compared to the corresponding control). In M-O, among the rare groups, Alpha  
318 increased notably in virus-enriched treatments without predators at 48h (+50% in enriched-0.8 $\mu$ -Tr).  
319 By contrast, nanoflagellates restrained their growth (-49.6% in 3 $\mu$ -Tr compared to the 0.8 $\mu$ -Tr  
320 control), and even more so after viral enrichment (-76.2% in enriched-3 $\mu$ -Tr) (Fig. 4). Conversely,  
321 the combined effect of nanoflagellates and viruses resulted in an increase of Beta cells at 12h  
322 (enriched-3 $\mu$ -Tr) while the presence of flagellates alone reduced Beta growth (3 $\mu$ -Tr versus 0.8 $\mu$ -  
323 Tr). At 48h, this pattern was reversed: Beta cells increased in the presence of flagellates (+112%  
324 compared to the control) while they decreased with additional viral enrichment (-50%).

325

## 326 **Discussion**

327 For each site, the survey concerned only one year without taking into account the potential inter-  
328 annual variability of microbial dynamics in the pattern of trophic succession (Guarini et al., 2004;  
329 Glé et al., 2007). Unfortunately, due to logistic restrictions, the comparison of the bays had to be  
330 carried out for two adjacent years, and the bias of inter-annual variability cannot be assessed.

331 After *in situ* surveys of one year, 48h *in vitro* incubation experiments were performed with different  
332 water categories treated by differential filtration, corresponding to a top-down manipulation of  
333 microbial compartments and consequently the removal of predators. Because of the complexity of  
334 the microbial food web, with parameters such as predation/competition links and the size overlap of  
335 predators and competitors, the size-fractionation method may reduce or eliminate some elements of  
336 normal trophic webs. Currently employed methods, including artificially composed trophic webs,

337 necessarily simplify natural systems. We consider that, of those currently employed, the filtration  
338 method is one which involves the least disturbance of the webs (Chen et al., 2009).

339

#### 340 *Temporal trophic succession*

341 Several previous studies have analysed seasonal production patterns in Arcachon Bay (Arc) (Robert  
342 et al., 1987; Glé et al., 2008) and Marennes Bay (M-O) (Guarini et al., 1998; Struski and Bacher,  
343 2006). In Arc, river runoff and high levels of tidal exchange create a gradient of nutrients along the  
344 basin, except for phosphate (Glé et al., 2008). Seasonally, as in our study, Arc is early nutrient  
345 limited with a depletion of nitrate from May to the autumn and of phosphate during spring. In M-O,  
346 nutrient availability was higher and limitations were only encountered episodically during certain  
347 years (Soletchnik et al., 1998; Struski, 2005). However, during our 2006 *in situ* survey, no  
348 limitations were found. Based on our multivariate analysis, Arc is spatially heterogeneous while M-  
349 O is spatially homogeneous, despite the influence of the Charente River. Moreover, as already  
350 illustrated by Soletchnik et al. (2007), seasonal variations, characterized by changes in salinity,  
351 temperature and chl<sub>a</sub> are higher in M-O than in Arc.

352 Our trophic organization framework was based on microbiological and environmental dynamics, as  
353 proposed by Legendre and Rassoulzadegan (1995). Mousseau et al. (2001) illustrated the  
354 periodicity of trophic organization using ratios of biomasses, production and uptake rates. For the  
355 present study, the entire spectrum of abundance from virioplankton to mesozooplankton were used  
356 in a similar manner to Rodriguez et al. (2000). We used microbial abundance instead of biomass  
357 since the contact rates between virus/host cells or prey/predator determine viral infections and  
358 grazing rates. Our empirical trophic-period definitions were validated by a factorial discriminant  
359 analysis (FDA) in which the discriminant variable was the defined trophic model (Fig. S1). The  
360 clusters remained separated even in the absence of the abundance data used for characterizing the  
361 trophic organization (Lambda Wilks test,  $p < 0.05$ ).

362 The microbial food web dominated in the two bays for 54% and 43% of the seven months of the  
363 surveys in Arc and M-O, respectively; although this consisted of short periods of domination in M-  
364 O and only 2 long ones in Arc. This domination was longer than what has been found in other  
365 coastal sites: on the Canadian East coast and in Plymouth Channel, the microbial food web  
366 dominated for less than 20% of the year and only during summer (Rodriguez et al., 2000; Mousseau  
367 et al., 2001). A herbivorous food web dominated in Canada for 50% of the year while it represented  
368 only 15% (2 short phytoplankton blooms) in Plymouth Channel. In the latter, there was a  
369 domination of the transition model i.e. the multivorous food web. In our study sites, the herbivorous  
370 web persisted over longer periods in M-O (43% of the first seven months) while the transitional  
371 multivorous web dominated in Arc (22% over the same period). The trophic systems of Arc, a  
372 largely closed lagoon, appear to be more stable and less subject to trophic variations than the more  
373 open M-O (Fig. 2; see also Fig. 4 in Soletchnik et al., (2007). In the latter, there was a succession of  
374 microbial and herbivorous models without a systematic passage through the transitional  
375 multivorous model. Moreover, the microbial food web was easier to distinguish from the other webs  
376 than in Arc (Fig. S1). Consequently, the dominance of the microbial food web attests the  
377 importance of microbial compartments in both ecosystems.

378 Another major difference between the bays is the contrasting trophic organization during winter: a  
379 herbivorous food web in Arc and a microbial food web in M-O. The presence of winter blooms has  
380 already been described in the Bay of Biscay (Labry et al., 2001; Marquis et al., 2007) and suggested  
381 for the two basins through analyses of long-term data series (Soletchnik et al., 2007). These  
382 phytoplankton blooms are influenced neither by temperature nor by nitrogen or phosphorus  
383 availability but are probably due to silicate input combined with a potential for salinity stratification  
384 or light availability.

385 The spring phytoplankton bloom occurred at the same period in both bays (April-May) yet it was  
386 greater in Arc, where it consisted of large phytoplankton forms such as diatoms and picoplankton.  
387 However, estimations of pelagic primary production illustrate a higher annual productivity in M-O



388 of 185  $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  compared with 103  $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  in Arc (Struski and Bacher, 2006; Glé et al.,  
389 2008).

390

### 391 *Grazing and viriolytic control*

392 Our results demonstrate that primary producers (small and large phytoplankton cells) and  
393 autotrophy-based mechanisms (cf. PCA results) are important in Arcachon Bay (Arc). However,  
394 Marennes Bay (M-O) is characterized by a higher potential for primary production, suggesting an  
395 uncoupling between phytoplankton abundance and productivity. The difference in phytoplankton  
396 abundance could be typically explained by (1) pelagic and benthic metazoan grazing, which is  
397 relatively low in M-O (Sautour and Castel, 1998) compared to Arc; (2) flushing out, which is  
398 relatively higher in M-O because it is quite an open system; (3) settling (Sautour and Castel, 1993);  
399 (4) light limitation (Pomeroy and Deibel, 1986; Sautour and Castel, 1993) and trophic status (meso-  
400 eutrophic in M-O vs. mesotrophic in Arc).

401 In addition, we show that in M-O, phytoplankton could also be controlled by viruses; this is  
402 corroborated by the simultaneous virus-bacteria uncoupling (Fig. 2). Viruses have been shown to  
403 modify the taxonomic diversity of their host communities, i.e. prokaryotes (Thingstad and Lignell,  
404 1997), and protists (Suttle, 2007) restraining the rapidly growing and succeeding species. Moreover,  
405 these successions of active phage-host systems would maintain a relatively constant baseline of host  
406 standing stocks (Wommack and Colwell, 2000). In addition, in M-O, virus infection could maintain  
407 the phytoplankton standing stock baseline at a low level. Thus, viral production may rely on  
408 autotroph lysis as well as bacterial lysogeny events. Moreover, the *in vitro* experiments show that,  
409 in the presence of protist predators, the potential for viral lysis of the bacteria standing stock was  
410 lower in M-O (2.6%) than in Arc (39%) during the phytoplankton bloom. Indeed, viral control of  
411 phytoplankton was less clear in Arc and the link between bacteria and viruses was strong. Without  
412 nanoflagellates, the release of large numbers of free viruses was in line with an increase in bacterial  
413 mortality of up to 70% of the bacterial standing stock, as already suggested by the contrasting

414 dynamics of nanoflagellates and viruses during the *in situ* survey (Fig. 2; Table 2). In contrast, the  
415 dynamics of nanoflagellates and viruses were similar in M-O, and during the spring bloom, virus-  
416 mediated bacterial mortality did not change significantly (9.4-13.6% with and without small  
417 nanoflagellates, respectively).

418 Thus, the two trophic models that prevailed during the phytoplankton spring bloom are also  
419 reflected in the interactions between the microbial compartments. The impact of nanoflagellates and  
420 viruses on picoplankton differs in a multivorous web (Arc) compared to a herbivorous web (M-O).

421 The *in vitro* experiments carried out in Arc showed that the strong potential for viral bacteriolysis  
422 (viral shunt: Wilhelm and Suttle, 1999) contributes to the development of picophytoeukaryotes  
423 (picoeuk) due to an increased supply of organic and inorganic nutrients. The presence of  
424 nanoflagellates, previously described as predators of picoeuk (Sherr and Sherr, 1994), appears to  
425 counteract the indirect positive effect of viruses on the latter. Thus, the contrasting effect of viruses  
426 and nanoflagellates on picoeuk can be defined as antagonist top-down control.

427 While the herbivorous web dominated in M-O, the antagonist impact could not be observed during  
428 *in vitro* experiments because of the very low abundance of picoeuk in the sampling water. The  
429 bacterioplankton were the only picoplankton compartment affected by viral enrichment in M-O:  
430 through the viral shunt, the absence of picoeuk reduces the competition for nutrients and thus  
431 increases the positive effect of viral enrichment on the growth of non-lysed bacteria.

432 In our study, nanoflagellate treatment in both bays did not affect bacterial abundance or growth, in  
433 contrast to published data (Zhang et al., 2007). However, this does not necessarily mean that  
434 predation by nanoflagellates had no effect. Indeed, flagellate grazing on picoeuk in Arc potentially  
435 released particulate organic matter, provoking the observed increase of bacterial proteolysis.  
436 Furthermore, with size-selective predation, the loss of bacteria through grazing is compensated by  
437 the growth of predation-resistant cells, suggesting that nanoflagellates can affect the phenotypic  
438 structure of bacterioplankton (Gonzalez et al., 1990; Monger and Landry, 1991; Simek et al., 1997;  
439 Posch et al., 1999). Moreover, considering the BCC data, the morphological diversity of bacteria

440 and the mean biovolumes of bacterial sub-populations, there should be a preferential grazing of  $\alpha$ -  
441 *proteobacteria* (small coccoid-shaped cells) by nanoflagellates compared to  $\beta$ -*proteobacteria* (large  
442 bacillus-shaped cells). Beta dominate in freshwater but can also be found in coastal waters, without  
443 a defined marine or riverine origin (Nold and Zwart, 1998). Indeed, they are present in both bays in  
444 proportions equivalent to more specifically marine groups like Alpha during spring phytoplankton  
445 blooms. More specifically, the hypothesis that Alpha are more vulnerable to grazing is confirmed in  
446 M-O. Moreover, Beta are not as opportunistic as Gamma but nevertheless are metabolically very  
447 reactive: the sensitivity of Alpha to grazing and to viral infection provides nutrients for Beta, which  
448 are resistant, and this is highlighted by an increase of bacterial proteolysis.

449 However, Beta were as vulnerable to grazing as Alpha in Arc. A different clonal composition of  
450 Beta could explain the variable response to predation pressure between the two bays (Brümmer et  
451 al., 2003; Schwalbach et al., 2004).

452 The variable responses of bacterial groups to viral lysis in the present study confirm previous results  
453 concerning BCC (Bouvier and Del Giorgio, 2007) and bacterial metabolism (Middelboe et al.,  
454 1996). Consequently, viral production can be modified according to the trophic period. During the  
455 multivorous phase of the phytoplankton spring bloom in Arc, viral production was synergistically  
456 depleted by the presence of flagellates and viral enrichment. The predation of picoeuk and bacteria  
457 decreases the number of host cells and could lead to a general drop of lytic or lysogenic viral  
458 production. Moreover, the acquisition of viral resistance, as observed with Alpha bacteria in virus-  
459 enriched incubation, would accentuate the negative impact on viral production. During the  
460 herbivorous phase of the phytoplankton spring bloom in M-O, the response in terms of viral  
461 production was the opposite. In the presence of flagellates, after virus enrichment, the development  
462 of predation-resistant and virus-sensitive Beta, at the expense of Alpha, led to a positive synergistic  
463 action of predators and viruses on viral production. This stimulation in the presence of flagellates  
464 has already been described (in contrast to the inhibition found in Arcachon) and explained by  
465 changes in BCC under grazing pressure (Simek et al., 2001; Weinbauer et al., 2003; Weinbauer et

466 al., 2007; Pradeep Ram and Sime-Ngando, 2008). Interestingly, our results also suggest that this  
467 stimulation occurs during the herbivorous period.

## 468 **Conclusion**

469 The temporal structure of trophic networks has been described in two bays on the French Atlantic  
470 coast, providing major new elements for future studies, in particular for comparing microbiological  
471 relationships during similar trophic periods.

472 Considering that trophic periods were defined in the same way for the two bays, the results of  
473 picoplankton and viral production can be extrapolated in relation to how multivorous and  
474 herbivorous trophic models work in general. Thus, during a multivorous period, viral lysis together  
475 with flagellate grazing may reduce viral production and act antagonistically toward picoeukaryotes.  
476 During a herbivorous period, flagellates and virus could both stimulate viral production. These  
477 contrasting responses sustain the debate about potential shifts in viral production due to grazing:  
478 positive or undetectable responses have already been found (Hornak et al., 2005; Weinbauer et al.,  
479 2007). For the first time, a negative effect of flagellate predation and viral lysis on viral production  
480 has been described and linked to a trophic model, the multivorous food web.

481

## 482 **Experimental procedures**

### 483 *Study site and sampling strategy of in situ surveys*

484 The study was carried out in two sites along the Bay of Biscay on the French Atlantic coast,  
485 Arcachon Bay and Marennes Oleron Bay, which are 150 km apart. Both are shallow, soft-bottom  
486 bays that are under strong tidal influence (Fig. S2). Arcachon Bay (44°40N, 1°10W) is a 180 km<sup>2</sup>  
487 triangular shaped coastal lagoon that communicates with the Atlantic through a broad channel to the  
488 south (Fig. S2). The Leyre River is the major source of freshwater for the lagoon (100 000 m<sup>3</sup>.y<sup>-1</sup>;  
489 Glé et al., 2007) which has a meso- to macrotidal regime with amplitudes from 1.1m to 4.9m. It is  
490 about 25 m deep at the entrance but the inside channels are shallow (5-10 m) , while about 70% of  
491 the bay is covered by intertidal flats (Blanchet et al., 2008). The water residence time is more than

492 3 weeks in the South East part of the bay. Marennes Oleron Bay to the North (46°00N, 1°10W) is  
493 similar in size (175 km<sup>2</sup>) and depth (mean=8.6m; Stanisière et al., 2006), and intertidal mudflats  
494 cover about 60% of its surface (Fig. S2). Freshwater arrives mainly from the Charente River, with  
495  $3 \times 10^9 \text{ m}^3 \cdot \text{y}^{-1}$ , or 90% of the total freshwater input (DDE-Charente Maritime/HYDRO-MEDD/DE).  
496 The bay is characterised by a macrotidal system, with amplitudes from 2 to 6m. It communicates  
497 with the ocean through two passes, the Pertuis de Maumusson to the South and the Pertuis  
498 d'Antioche to the North, with a relatively short residence time of 11 days. Tidal exchanges are  
499 greater through the northern pass, resulting in a north-south circulation of oceanic (Bay of Biscay)  
500 water (Struski, 2005).

501 Sampling was carried out twice weekly, from January to August 2005, at 2 stations in Arcachon  
502 Bay: B13, near the mouth of the Bay, which is under oceanic influence, and Comprian, in the inner  
503 basin, which is affected by the continental runoff. Five stations were surveyed in Marennes Oleron  
504 Bay on a bi-monthly basis (January to December 2006). The stations were spread out over the entire  
505 basin: one was close to the southern pass (A= Auger), two were above mudflats close to the  
506 continent (Br=Brouage) and island (O= Oleron) coasts, one was close to the northern pass  
507 (B=Boyard) and one near the mouth of the Charente River (C=Charente).

508 Water samples were collected in both bays near the surface (<1m) using Niskin bottles. Subsamples  
509 were fixed on board. The rest were kept in 8L polypropylene dark bottles for laboratory analyses  
510 (transfer time <3h). Physical parameters (temperature, salinity, pH) were recorded on board with  
511 multiparameter probes (Seabird SBE25 in Arcachon and YSI 6600EDS-M in Marennes).

512

### 513 *Batch culture design*

514 Experimental water was collected at high tide at the surface from the central Comprian station in  
515 Arcachon Bay on 17 May 2006 and from the northern “E” station in Marennes Bay (Fig. S2) on 24  
516 April 2007. The experimental protocols were based on a slightly modified version of the method of  
517 Auguet et al. (2009). In the lab, three water categories were obtained by sequential filtration from

518 75L of seawater: (1) <20µm, filtered through nylon membranes, (2) <3µm, filtered through  
519 Versapor acrylic polymer membranes (Gelman Sciences Inc.) and (3) <0.8µm, filtered through  
520 cellulose acetate membranes (Sartorius). Viral particles were then concentrated from 40L of <0.2-  
521 water, as a high molecular weight concentrate (HMWC) using a 30kDa polysulfone cartridge  
522 (Sartorius). Viral-free water was kept for use as dilution water. Six different treatments were  
523 prepared with the three water categories (Table 3), each diluted ten fold with the dilution water and  
524 enriched (x2) or not with viruses (HMWC).

525 Each of the six treatments were triplicated in 2.4L Nalgene polycarbonate bottles filled with 2200  
526 ml and incubated under *in situ* conditions of light and temperature in circulating seawater tanks.  
527 Samples for bacterial, viral, phytoplankton and flagellate counts were collected at 0, 6, 12, 18, 24,  
528 38 and 48h. Samples for bacterial activity and diversity were collected every 12h. Samples for  
529 ciliate abundance were collected at the beginning and the end of the experiment (<20µm treatment).

530

#### 531 *Physical and chemical parameters*

532 Seston was assessed by filtering 200 to 500 ml of water according to turbidity and processed  
533 according to Auguet et al. (2005). Samples for dissolved inorganic nutrients (Silicate (Si),  
534 Phosphate (PO<sub>4</sub>), Urea, Ammonium (NH<sub>4</sub>), Nitrite (NO<sub>2</sub>) and Nitrate (NO<sub>3</sub>)) were filtered (20ml,  
535 Whatman GF/F) into glass flasks and stored at -20°C for analyses with an autoanalyser (Bran and  
536 Luebbe, AA3 for Arcachon and Skalar for Marennes (Strickland and Parsons, 1972)).

537

#### 538 *Biological parameters*

539 Chlorophyll *a* (chl<sub>a</sub>) and pheopigment were analysed by filtering 200 ml of water through Whatman  
540 GF/F filters (25 mm). Filters were stored for less than a month at -20°C before extraction (acetone  
541 90% overnight at 4°C and shaken). Samples were analysed by the fluorimetry method (Turner, TD  
542 700) according to Yentsch and Menzel (1963).

543 Subsamples (3ml) for viral and bacterial counts were fixed with 0.02- $\mu\text{m}$  filtered formaldehyde (2%  
544 final concentration) and stored for less than a week at 4°C. Samples were enumerated by  
545 epifluorescence microscopy after staining for 30 min with Sybr Green I (Noble and Fuhrman, 1998).  
546 Bacteria and viruses were counted in at least 15 fields chosen randomly under blue excitation (Zeiss  
547 Axioskop 1000x). Using flow cytometry (FACSCalibur, Bektom Dickinson) and Sybr-GreenI  
548 staining, bacteria cells were distinguished between High Nucleic Acid (HNA) and Low Nucleic  
549 Acid (LNA) cells. Furthermore, for batch culture samples, HNA cells were clustered in 4 sub-  
550 groups (populations 3, 4, 5 and 6) according to decreasing biovolume (2, 0.8, 0.3 and 0.15  $\mu\text{m}^3$ ,  
551 respectively) and fluorescence. Small phytoplankton cells (<10 $\mu\text{m}$ ; picoeukaryotes, nanoeukaryotes  
552 and *Synechococcus*) were analysed using flow cytometry according to Joux et al. (2005).  
553 Microphytoplankton (>10 $\mu\text{m}$ ) and ciliate subsamples were fixed and stained in alkaline lugol (final  
554 concentration, 1%). 10-20 ml subsamples were decanted in Utermöhl settling chambers before  
555 counting and sizing by inverted microscopy (white light, Leica DMIRB, 400x – 630x). For ciliate  
556 samples, the suspended matter of a 1L subsample was settled for 6h at *in situ* temperature before  
557 siphoning off the top 850ml and fixing a 150ml aliquot of the siphoned water. Nanoflagellates  
558 (60ml) were fixed with paraformaldehyde (final concentration 1%) and stored at 4°C for less than a  
559 week. Cells filtered onto 0.8 $\mu\text{m}$  black polycarbonate membranes (Nucleopore) were stained with  
560 DAPI (Porter and Feig, 1980) and counted under ultraviolet excitation (Zeiss Axioskop 1000x) with  
561 a distinction between unpigmented (HNF) and pigmented (ANF) nanoflagellates based on the  
562 absence of chlorophyll fluorescence under green excitation. At least 100 nanoflagellates were  
563 counted for each slide.

564 Mesozooplankton were collected 1m below the surface in Arcachon Bay using a standard 200 $\mu\text{m}$   
565 WP-2 net towed slowly against the current. The catch was fixed in 5% seawater/formalin and  
566 counted with a binocular loupe.

567

568

569 *Bacterial growth, viral production and bacterial mortality*

570 The maximum specific growth rate ( $\text{h}^{-1}$ ) of bacteria was calculated from log transformed abundance  
571 data during the exponential growth phase in each bottle. Total viral production rate ( $\text{h}^{-1}$ ) was  
572 calculated by adding the net increase of logarithmic viral abundance during each peak divided by  
573 the incubation time. The bacterial mortality ( $\text{cell.ml}^{-1}.\text{h}^{-1}$ ) induced by viral lysis was determined in  
574 unenriched treatments from the viral production (sum of the net increase of viral abundance divided  
575 by the duration of the experiment,  $\text{particles.ml}^{-1}.\text{h}^{-1}$ ) divided by an assumed burst size of 50. The  
576 percentage of bacterial cells lysed ( $\text{d}^{-1}$ ) was equivalent to the bacterial mortality rate ( $\text{cell.ml}^{-1}.\text{d}^{-1}$ )  
577 divided by the total bacterial abundance.

578

579 *Bacterial activity*

580 Leucine aminopeptidase activity was measured in duplicate at T0, 12, 24, 36 and T48h by using L-  
581 Leucine-7-amino-4-methylcoumarin hydrochloride (Leu-MCA, Sigma) as a model protein substrate,  
582 according to Hoppe (1993). The enzyme  $V_{\text{max}}$  was determined by adding substrate to the sample,  
583 giving a final saturating concentration of  $1000\mu\text{M}$ . Incubations were performed in the dark and at *in*  
584 *situ* temperature for around 5h, then stopped using Sodium-dodecyl sulfate (1% final concentration)  
585 The release of 7-amino-4-methylcoumarin dye (MCA, Sigma) was measured with a  
586 spectrofluorometer (Kontron, model SFM 25) at 380nm excitation and 440nm emission. Solutions  
587 of MCA (20 to 2000nM) were used as a standard for calibration. The potential enzymatic activity  
588 per cell was obtained by dividing  $V_{\text{max}}$  by the corresponding bacterial abundance (specific  $V_{\text{max}}$ ,  
589  $\text{fM.cell}^{-1}.\text{h}^{-1}$ ).

590

591 *Bacterial diversity*

592 Bacterial community composition was determined with fluorescent *in situ* hybridization using eight  
593 Cy-3 labelled probes (MWG-Biotech): a mix of Eub 338 I,II and III for Eubacteria, Pla5a for  
594 Planctomycetes, CF319a for Cytophaga-Flavobacterium cluster, Alf1b for  *$\alpha$ -proteobacteria*, Bet43a



595 for *β-proteobacteria*, Gam42a for *γ-proteobacteria*, Arch915 for *archaea* and a non specific probe  
596 as a control (Amann et al., 1995; Bouvier and Del Giorgio, 2007).

597 Samples were fixed in paraformaldehyde (2% final) and stored for at least 12h at 4°C before  
598 freezing at -20°C. Bacteria were filtered onto 0.2µm polycarbonate membranes (Whatman), rinsed  
599 with 0.2µm-filtered milli-Q water, dried and stored at -20°C. Pieces of membrane were hybridized  
600 with 9µl of hybridization solution (Cy3-labelled probe, 2.5ng.µl<sup>-1</sup>) for 4h30 at 46°C and washed at  
601 48°C for 15 mn. The membrane was then rinsed for a few seconds successively in 0.2µm-filtered  
602 Milli-Q water then 80% ethanol and finally air dried. Bacterial cells were counter-stained with  
603 DAPI mounting solution (0.25µg.µl<sup>-1</sup> in (Citifluor (Biovalley)/Vectashield (Ablys, SA, Paris): 4/1).  
604 At least 10 fields were counted on an epifluorescence microscope (Axioskop, Zeiss) using Cy3  
605 (blue) and DAPI (UV) filters.

606

#### 607 *Identification of trophic dynamics*

608 Trophic periods were defined empirically using the 4 conceptual trophic flux models of Legendre  
609 and Rassoulzadegan (1995), primarily from the abundances of phytoplankton and bacteria but also  
610 taking into account the dynamics of viruses, HNF and ciliates (Table 4).

611 The herbivorous food web is characterized by blooms of large (>10µm) phytoplankton cells. During  
612 this period there is in general an increase in the number of ciliates. The microbial food web is  
613 defined by an increase of small autotrophs (phytoplankton <10µm) and heterotrophs (bacteria).  
614 Their potential predators (HNF and ciliates) may increase in number. The microbial loop, a closed  
615 system maintained by nutrient regeneration, is characterized by high abundance of exclusively  
616 heterotrophic micro-organisms (bacteria, HNF and ciliates). Finally, the multivorous food web is a  
617 transitional model where all trophic pathways are actively contributing to the dynamics of the  
618 ecosystem.

619 The trophic organization identified for each bay was then formalized using multivariate factorial  
620 discriminant analysis (FDA). FDA classifies the samples using predefined criteria (i.e. the trophic

621 model) to discriminate samples according to independent variables (all abiotic and biotic  
622 parameters). Prior to the FDA analysis, data were normalized and tested for heteroskedasticity  
623 (Levene test, Ho: equal variances between criteria). The purpose was to test whether samples are  
624 classified as predicted by the empirical trophic model and to assess the relative importance of the  
625 independent variables in the classification. The significance of clustering is tested by a Wilks  
626 Lambda test (low Lambda values corresponds to significant ( $p < 0.05$ ) clustering).

627

### 628 *Statistical analysis*

629 To compare field data between the 2 bays, the Arcachon results (3-day intervals) were regrouped by  
630 sliding means to obtain 15-day time steps, as in Marennes Bay. Statistical analyses were performed  
631 with log transformed data using XLStat (Addinsoft; version 7.5.2: one way- or two way-ANOVA,  
632 simple regression, Principal Component Analysis (PCA) combined with Hierarchical Ascendant  
633 Classification (HAC), Factorial Discriminant Analysis (FDA)) and Minitab (version 15: stepwise  
634 multiple regressions and Levene test for Heteroskedasticity).

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### 641 **References**

- 642 Allard, J., Chaumillon, E., and Féliès, H. (2009) A synthesis of morphological evolutions and  
643 Holocene stratigraphy of a wave-dominated estuary: The Arcachon lagoon, SW France. *Continental*  
644 *Shelf Research*.
- 645 Amann, R.L., Ludwig, W., and Schleifer, K.-H. (1995) Phylogenetic identification and in situ  
646 detection of individual microbial cells without cultivation. *Microbiological Reviews* **59**: 143-169.
- 647 Auguet, J.C., Montanie, H., Delmas, D., Hartmann, H.J., and Huet, V. (2005) Dynamic of  
648 virioplankton abundance and its environmental control in the Charente estuary (France). *Microbial*  
649 *Ecology* **50**: 337-349.

- 650 Auguet, J.C., Montanie, H., Hartmann, H.J., Lebaron, P., Casamayor, E.O., Catala, P., and Delmas,  
651 D. (2009) Potential effect of freshwater virus on the structure and activity of bacterial communities  
652 in the Marennes-Oléron Bay (France). *Microbial Ecology* **57**: 295-306.
- 653 Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., and Thingstad, T.F. (1983) The  
654 ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* **10**: 257-263.
- 655 Baudoux, A.-C., Veldhuis, M.J.W., Noordeloos, A.A.M., van Noort, G., and Brussaard, C.P.D.  
656 (2008) Estimates of virus- vs. grazing induced mortality of picophytoplankton in the North Sea  
657 during summer. *Aquat Microb Ecol* **52**: 69-82.
- 658 Blanchet, H., Lavesque, N., Ruellet, T., Dauvin, J.C., Sauriau, P.G., Desroy, N. et al. (2008) Use of  
659 biotic indices in semi-enclosed coastal ecosystems and transitional waters habitats—Implications  
660 for the implementation of the European Water Framework Directive. *Ecological Indicators* **8**: 360-  
661 372.
- 662 Boehme, J., Frischer, M.E., Jiang, S.C., Kellogg, C.A., Pichrad, S., Rose, J.B. et al. (1993) Viruses,  
663 bacterioplankton, and phytoplankton in the southeastern Gulf of Mexico: distribution and  
664 contribution to oceanic DNA pools. *Marine ecology progress series* **97**: 1-10.
- 665 Boras, J.A., Sala, M.M., Vazquez-Dominguez, E., Weinbauer, M.G., and Vaque, D. (2009) Annual  
666 changes of bacterial mortality due to viruses and protists in an oligotrophic coastal environment  
667 (NW Mediterranean). *Environmental Microbiology* **11**: 1181-1193.
- 668 Borsheim, K.Y., Bratbak, G., and Heldal, M. (1990) Enumeration and biomass estimation of  
669 planktonic bacteria and viruses by transmission electron microscopy. *Applied and environmental*  
670 *microbiology* **56**: 352-356.
- 671 Bouvier, T., and Del Giorgio, P.A. (2007) Key role of selective viral-induced mortality in  
672 determining marine bacterial community composition. *Environmental Microbiology* **9**: 287-297.
- 673 Brümmer, I.H.M., Felske, A., and Wagner-Döbler, I. (2003) Diversity and seasonal variability of  
674 beta-proteobacteria in biofilms of polluted rivers: analysis by temperature gradient gel  
675 electrophoresis and cloning. *Applied and environmental microbiology* **69**: 4463-4473.
- 676 Calbet, A., and Saiz, E. (2005) The ciliate-copepod link in marine ecosystems. *Aquatic Microbial*  
677 *Ecology* **38**: 157-167.
- 678 Chen, B., Liu, H., and Wang, Z. (2009) Trophic interactions within the microbial food web in the  
679 South China Sea revealed by size-fractionation method. *Journal of Experimental Marine Biology*  
680 *and Ecology* **368**: 59-66.
- 681 Cottrell, M.T., and Suttle, C.A. (1995) Dynamics of a lytic virus infecting the photosynthetic  
682 marine picoflagellate *Micromonas pusilla*. *Limnology and Oceanography* **40**: 730-739.
- 683 Fuhrman, J.A. (1999) Marine viruses and their biogeochemical and ecological effects. *Nature* **399**:  
684 541-548.
- 685 Fuhrman, J.A. (2009) Microbial community structure and its functional implications. *Nature* **459**:  
686 193-199.
- 687 Garza, D.R., and Suttle, C.A. (1995) Large double-stranded DNA viruses which cause the lysis of a  
688 marine heterotrophic nanoflagellate (*Bodo* sp.) occur in natural marine viral communities. *Aquatic*  
689 *Microbial Ecology* **9**: 203-210.
- 690 Gasol, J.M., Pedros-Alio, C., and Vaque, D. (2002) Regulation of bacterial assemblages in  
691 oligotrophic plankton systems: results from experimental and empirical approaches. *Antonie Van*  
692 *Leeuwenhoek* **81**: 435-452.

- 693 Glé, C., Del Amo, Y., Sautour, B., Laborde, P., and Chardy, P. (2008) Variability of nutrients and  
694 phytoplankton primary production in a shallow macrotidal coastal ecosystem (Arcachon Bay,  
695 France). *Estuarine, Coastal and Shelf Science* **76**: 642-656.
- 696 Glé, C., Del Amo, Y., Bec, B., Sautour, B., Froidefond, J.-M., Gohin, F. et al. (2007) Typology of  
697 environmental conditions at the onset of winter phytoplankton blooms in a shallow macrotidal  
698 coastal ecosystem, Arcachon Bay (France). *Journal of Plankton Research* **29**: 999-1014.
- 699 Gonzalez, J.M., Sherr, E.B., and Sherr, B.F. (1990) Size-selective grazing on bacteria by natural  
700 assemblages of estuarine flagellates and ciliates. *Applied and environmental microbiology* **56**: 583-  
701 589.
- 702 Guarini, J.-M., Gros, P., Blanchard, G.F., Richard, P., and Fillon, A. (2004) Benthic contribution to  
703 pelagic microalgal communities in two semi-enclosed, European-type littoral ecosystems  
704 (Marennes-Oléron Bay and Aiguillon Bay, France). *Journal of Sea Research* **52**: 241-258.
- 705 Guarini, J.-M., Blanchard, G.F., Bacher, C., Gros, P., Riera, P., Richard, P. et al. (1998) Dynamics  
706 of spatial patterns of microphytobenthic biomass: inferences from a geostatistical analysis of two  
707 comprehensive surveys in Marennes-Oléron Bay (France). *Marine Ecology Progress Series* **166**:  
708 131-141.
- 709 Guixa-Boixereu, N., Vaqué, D., Gasol, J.M., and Pedros-Alio, C. (1999) Distribution of viruses and  
710 their potential effect on bacterioplankton in an oligotrophic marine system. *Aquat Microb Ecol* **19**:  
711 205-213.
- 712 Hahn, M.W., and Hofle, M.G. (2001) Grazing of protozoa and its effect on populations of aquatic  
713 bacteria. *FEMS Microbiology Ecology* **35**: 113-121.
- 714 Hennes, K., P., and Suttle, C.A. (1995) Direct counts of viruses in natural waters and laboratory  
715 cultures by epifluorescence microscopy. *Limnology and Oceanography* **40**.
- 716 Hirose, M., Katano, T., and Nakano, S.-I. (2008) Growth and grazing mortality rates of  
717 *Prochlorococcus*, *Synechococcus* and eukaryotic picophytoplankton in the bay of the Uwa Sea,  
718 Japan. *Journal of Plankton Research* **30**: 241-250.
- 719 Hoppe, H.G. (1993) Use of fluorogenic model substrates for extracellular enzyme activity (EEA) of  
720 bacteria. In *Handbook of methods in Aquatic Microbial Ecology*. Kemp, P.F., Sherr, B.F., Sherr,  
721 E.B., and Cole, J.J. (eds). Boca Raton, FL: Lewis Publishers, pp. 423-431.
- 722 Hornak, K., Masin, M., Jezbera, J., Bettarel, Y., Nedoma, J., Sime-Ngando, T., and Simek, K. (2005)  
723 Effects of decreased resource availability, protozoan grazing and viral impact on the structure of  
724 bacterioplankton assemblage in a canyon-shaped reservoir. *FEMS Microbiology Ecology* **52**: 315-  
725 327.
- 726 Joux, F., Servais, P., Naudin, J.-J., Lebaron, P., Oriol, L., and Courties, C. (2005) Distribution of  
727 picophytoplankton and bacterioplankton along a river plume gradient in the Mediterranean Sea. *Vie*  
728 *et Milieu* **55**: 197-208.
- 729 Kirchman, D.L., Meon, B., Cottrell, M.T., Hutchins, D.A., Weeks, D., and Bruland, K.W. (2000)  
730 Carbon versus iron limitation of bacterial growth in the California upwelling regime. *Limnol*  
731 *Oceanogr* **45**: 1681-1688.
- 732 Labry, C., Herbland, A., Delmas, D., Laborde, P., Lazure, P., Froidefond, J.-M. et al. (2001)  
733 Initiation of winter phytoplankton blooms within the Gironde plume waters in the Bay of Biscay.  
734 *Marine Ecology Progress Series* **212**: 117-130.
- 735 Legendre, L., and Rassoulzadegan, F. (1995) Plankton and nutrient dynamics in marine waters.  
736 *Ophelia* **41**: 153-172.
- 737 Li, W.K.W. (1998) Annual average abundance of heterotrophic bacteria and *Synechococcus* in  
738 surface ocean waters. *Limnology and Oceanography* **43**: 1746-1753.

- 739 Maranger, R., Bird, D.F., and Juniper, S.K. (1994) Viral and bacterial dynamics in Arctic sea ice  
740 during the spring algal bloom near Resolute, N.W.T., Canada. *Marine Ecology Progress Series* **111**:  
741 121-127.
- 742 Marquis, E., Niquil, N., Delmas, D., Hartmann, H.J., Bonnet, D., Carlotti, F. et al. (2007) Inverse  
743 analysis of the planktonic food web dynamics related to phytoplankton bloom development on the  
744 continental shelf of the Bay of Biscay, French coast. *Estuarine, Coastal and Shelf Science* **73**: 223-  
745 235.
- 746 Massana, R., Del Campo, J., Dinter, C., and Sommaruga, R. (2007) Crash of a population of the  
747 marine heterotrophic flagellate *Cafeteria roenbergensis* by viral infection. *Environmental*  
748 *Microbiology* **9**: 2660-2669.
- 749 Middelboe, M., Jorgensen, N.O.G., and Kroer, N. (1996) Effects of viruses on nutrients turnover  
750 and growth efficiency of non-infected marine bacterioplankton. *Applied and Environmental*  
751 *Microbiology* **62**: 1991-1997.
- 752 Monger, B.C., and Landry, M.R. (1991) Prey-size dependency of grazing by free-living marine  
753 flagellates. *Marine Ecology Progress Series* **74**: 239-248.
- 754 Monger, B.C., Landry, M.R., and Brown, S.L. (1999) Feeding selection of heterotrophic marine  
755 nanoflagellates based on the surface hydrophobicity of their picoplankton prey. *Limnology and*  
756 *Oceanography* **44**: 1917-1927.
- 757 Mousseau, L., Klein, B., Legendre, L., Dauchez, S., Tamigneaux, E., Tremblay, J.-E., and Grant  
758 Ingram, R. (2001) Assessing the trophic pathways that dominate planktonic food webs: an approach  
759 based on simple ecological ratios. *Journal of Plankton research* **23**: 765-777.
- 760 Nielsen, T.G., and Kiorboe, T. (1994) Regulation of zooplankton biomass and production in a  
761 temperate, coastal system. 2. Ciliates. *Limnology and Oceanography* **39**: 508-519.
- 762 Noble, R.T., and Fuhrman, J.A. (1998) Use of SYBR Green I for rapid epifluorescence counts of  
763 marine viruses and bacteria. *Aquatic Microbial Ecology* **14**: 113-118.
- 764 Nold, S., and Zwart, G. (1998) Patterns and governing forces in aquatic microbial communities.  
765 *Aquatic Ecology* **32**: 17-35.
- 766 Platt, T., Subba Rao, D.V., and Irwin, B. (1983) Photosynthesis of picoplankton in the oligotrophic  
767 ocean. *Nature* **301**: 702-704.
- 768 Pomeroy, L.R., and Deibel, D. (1986) temperature regulation of bacterial activity during the spring  
769 bloom in newfoundland coastal waters. *Science* **233**: 359-361.
- 770 Porter, K.G., and Feig, Y.S. (1980) The use of DAPI for identifying and counting aquatic  
771 microflora. *Limnology and Oceanography* **25**: 943-948.
- 772 Posch, T., Jezbera, J., Vrba, J., Simek, K., Pernthaler, J., Andreatta, S., and Sonntag, B. (2001) Size  
773 selectivity feeding in *Cyclidium glaucoma* (Ciliophora, Scuticociliatida) and its effects on bacterial  
774 community structure: a study from a continuous cultivation system. *Microbial Ecology* **42**: 217-227.
- 775 Posch, T., Simek, K., Vrba, J., Pernthaler, J., Nedoma, J., Sattler, B. et al. (1999) Predator-induced  
776 changes of bacterial size-structure and productivity studied on an experimental microbial  
777 community. *Aquatic microbial ecology* **18**: 235-246.
- 778 Pradeep Ram, A., and Sime-Ngando, T. (2008) Functional responses of prokaryotes and viruses to  
779 grazer effects and nutrient additions in freshwater microcosms. *The ISME Journal* **2**: 498-509.
- 780 Rivkin, R.B., Legendre, L., Deibel, D., Tremblay, J.-E., Klein, B., Crocker, K. et al. (1996) Vertical  
781 flux of biogenic carbon in the ocean: Is there food web control? *Science* **272**: 1163-1166.
- 782 Robert, R., Guillocheau, N., and Collos, Y. (1987) Hydrobiological parameters during an annual  
783 cycle in the Arcachon Basin. *Marine Biology* **95**: 631-640.

- 784 Rodriguez, F., Fernandez, E., Head, R.N., Harbour, D.S., Bratbak, G., Heldal, M., and Harris, R.P.  
785 (2000) Temporal variability of viruses, bacteria, phytoplankton and zooplankton in the western  
786 English Channel off Plymouth. *Journal of the Marine Biological Association of UK* **80**: 575-586.
- 787 Sanders, R.W., Caron, D.A., and Berninger, U.G. (1992) Relationships between bacteria and  
788 heterotrophic nanoplankton in marine and fresh waters: an inter-ecosystem comparison. *Marine ecology*  
789 *progress series* **86**: 1-14.
- 790 Sautour, B., and Castel, J. (1993) Distribution of zooplankton populations in Marennes-Oléron Bay  
791 (France), structure and grazing impact of copepod communities. *Oceanologica Acta* **16**: 279-290.
- 792 Sautour, B., and Castel, J. (1998) Importance of microzooplanktonic crustaceans in the coastal food  
793 chain: Bay of Marennes-Oléron, France. *Oceanologica Acta* **21**: 105-112.
- 794 Schwalbach, M.S., Hewson, I., and Fuhrman, J.A. (2004) Viral effects on bacterial community  
795 composition in marine plankton microcosms. *Aquatic Microbial Ecology* **34**: 117-127.
- 796 Sherr, E.B., and Sherr, B.F. (1988) Role of microbes in pelagic food webs: A revised concept.  
797 *Limnology and Oceanography* **33**: 1225-1227.
- 798 Sherr, E.B., and Sherr, B.F. (1994) Bacterivory and herbivory: Key roles of phagotrophic protists in  
799 pelagic food web. *Microbial Ecology* **28**: 223-235.
- 800 Simek, K., Vrba, J., Pernthaler, J., Posch, T., Hartman, P., Nedoma, J., and Psenner, R. (1997)  
801 Morphological and Compositional Shifts in an Experimental Bacterial Community Influenced by  
802 Protists with Contrasting Feeding Modes. *Applied and Environmental Microbiology* **63**: 587-595.
- 803 Simek, K., Pernthaler, J., Weinbauer, M.G., Hornak, K., Dolan, J.R., nedoma, J. et al. (2001)  
804 Changes in bacterial community composition and dynamics and viral mortality rates associated with  
805 enhanced flagellate grazing in mesoeutrophic reservoir. *Applied and environmental microbiology*  
806 **67**: 2723-2733.
- 807 Soletchnik, P., Faury, N., Razet, D., and Gouletquer, P. (1998) Hydrobiology of the Marennes-  
808 Oléron Bay. Seasonal indices and analysis of trends from 1978 to 1995. *Hydrobiologia* **386**: 131-  
809 146.
- 810 Soletchnik, P., Ropert, M., Mazurié, J., Fleury, P.G., and Le Coz, F. (2007) Relationships between  
811 oyster mortality patterns and environmental data from monitoring databases along the coasts of  
812 France. *Aquaculture* **271**: 384-400.
- 813 Stanisière, J.-Y., Dumas, F., Plus, M., Maurer, D., and Robert, S. (2006) Caractérisation des  
814 composantes hydrodynamiques d'un système côtier semi-fermé: Le Bassin de Marennes-Oléron. In  
815 *Thème 1: Caractérisation des forçages hydrodynamiques*. Atlantique, P.-C.L.A.m.d.f.d.s.s.-f.d.l.  
816 (ed).
- 817 Strickland, J.D.H., and Parsons, T.R. (eds) (1972) *A practical handbook of seawater analysis*:  
818 Fishery Research Board Canada.
- 819 Struski, C. (2005) Modélisation des flux de matières dans la baie de Marennes-Oléron: Couplage de  
820 l'hydrodynamisme, de la production primaire et de la consommation par les huîtres. *Thèse de*  
821 *doctorat d'état. Université de La Rochelle*: 306p.
- 822 Struski, C., and Bacher, C. (2006) Preliminary estimate of primary production by phytoplankton in  
823 Marennes-Oléron Bay, France. *Estuarine, Coastal and Shelf Science* **66**: 323-334.
- 824 Suttle, C.A. (2005) Viruses in the sea. *Nature* **437**: 356-361.
- 825 Suttle, C.A. (2007) Marine viruses-major players in the global ecosystem. *Nature Reviews*  
826 *Microbiology* **5**: 801-812.
- 827 Thingstad, T.F., and Lignell, R. (1997) Theoretical models for the control of bacterial growth rate,  
828 abundance, diversity and carbon demand. *Aquatic microbial ecology* **13**: 19-27.

- 829 Weinbauer, M.G., Christaki, U., Nedoma, J., and Simek, K. (2003) Comparing the effects of  
830 resource enrichment and grazing on viral production in a meso-eutrophic reservoir. *Aquatic*  
831 *Microbial Ecology* **31**: 137-144.
- 832 Weinbauer, M.G., Hornak, K., Jezbera, J., Nedoma, J., Dolan, J.R., and Simek, K. (2007)  
833 Synergistic and antagonistic effects of viral lysis and protistan grazing on bacterial biomass,  
834 production and diversity. *Environmental Microbiology* **9**: 777-788.
- 835 Wilhelm, S.W., and Suttle, C.A. (1999) Viruses and nutrient cycles in the sea. *Bioscience* **49**: 781-  
836 788.
- 837 Winter, C., Smit, A., Herndl, G.J., and Weinbauer, M.G. (2004) Impact of virioplankton on archaeal  
838 and bacterial community richness as assessed in seawater batch cultures. *Applied and*  
839 *environmental microbiology* **70**: 804-813.
- 840 Wommack, K.E., and Colwell, R.R. (2000) Virioplankton: Viruses in aquatic ecosystems.  
841 *Microbiology and molecular biology reviews* **64**: 69-114.
- 842 Yentsch, C.S., and Menzel, D.W. (1963) A method for the determination of phytoplankton  
843 chlorophyll and pheophytin by fluorescence. *Deep-sea Research* **10**: 221-231.
- 844 Zhang, R., Weinbauer, M.G., and Qian, P.Y. (2007) Viruses and flagellates sustain apparent  
845 richness and reduce biomass accumulation of bacterioplankton in coastal marine waters.  
846 *Environmental Microbiology* **9**: 3008-3018.
- 847
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849 **Table and figure legends:**

850

851

852 **Table 1:** Annual means and simple linear regressions between bacterioplankton (BA) and virioplankton (VA) at the sampling stations of Marennes  
 853 Oléron Bay (2006) and Arcachon Bay (2005). Linear regressions were performed with log transformed data.  
 854

	Stations	BA (cells.ml <sup>-1</sup> )	VA (particles.ml <sup>-1</sup> )	Equation	r <sup>2</sup>	p	n
Marennes	Auger	4.04x10 <sup>6</sup> (min-8.70x10 <sup>5</sup> /max-1.01x10 <sup>7</sup> )	3.18x10 <sup>7</sup> (min-5.24x10 <sup>6</sup> /max-5.97x10 <sup>7</sup> )	log BA= 1.5logVA-4.7	0.60	<0.0001	20
	Boyard	3.95x10 <sup>6</sup> (min-1.01x10 <sup>6</sup> /max-1.30x10 <sup>6</sup> )	3.36x10 <sup>7</sup> (min-1.82x10 <sup>7</sup> /max-5.59x10 <sup>7</sup> )	log BA= 1.45logVA-4.39	0.46	0.001	20
	Charente	4.60x10 <sup>6</sup> (min-1.16x10 <sup>6</sup> /max-1.17x10 <sup>7</sup> )	3.96x10 <sup>7</sup> (min-2.01x10 <sup>7</sup> /max-6.36x10 <sup>7</sup> )	log BA= 0.84logVA+0.23	0.18	0.092	17
	Oléron	3.70x10 <sup>6</sup> (min-1.05x10 <sup>6</sup> /max-9.03x10 <sup>6</sup> )	3.07x10 <sup>7</sup> (min-1.82x10 <sup>7</sup> /max-5.07x10 <sup>7</sup> )	log BA= 1.74logVA-6.51	0.45	0.001	20
	Brouage	4.28x10 <sup>6</sup> (min-7.10x10 <sup>5</sup> /max-1.8x10 <sup>7</sup> )	3.35x10 <sup>7</sup> (min-1.66x10 <sup>7</sup> /max-6.08x10 <sup>7</sup> )	log BA= 1.6logVA-5.5	0.51	0.001	19
Arcachon	B13	1.05x10 <sup>6</sup> (min-3.10x10 <sup>5</sup> /max-1.58x10 <sup>6</sup> )	4.48x10 <sup>6</sup> (min-7.50x10 <sup>5</sup> /max-8.11x10 <sup>6</sup> )	log BA= 0.6logVA+2.06	0.83	<0.0001	31
	Comprian	1.32x10 <sup>6</sup> (min-5.00x10 <sup>5</sup> /max-2.38x10 <sup>6</sup> )	6.70x10 <sup>6</sup> (min-1.44x10 <sup>6</sup> /max-1.01x10 <sup>7</sup> )	log BA= 0.47logVA+2.93	0.60	<0.0001	31

855

856



857 **Table 2.** Stepwise linear regression of bacteria, virus, flagellate and ciliate abundance according to environmental parameters in Arcachon and  
858 Marennes bays for the entire year and according to the season. The seasons were defined based on the PCA results. Descriptors: BA: Bacterial  
859 abundance, VA: Viral abundance, HNF: Heterotrophic nanoflagellate abundance, ANF: Autotrophic nanoflagellate abundance, HNA: Abundance of  
860 high nucleic acid bacteria, Cil: Ciliate abundance, Pico: Picoplankton abundance, Nano: Nanoplankton abundance, Syn: *Synechococcus* abundance,  
861 Dino: Dinophyceae abundance, Diat: Diatom abundance, Cop: Copepods abundance T°w: Water temperature, S%: Salinity, Crypto: Cryptophyceae  
862 abundance, Seston Org: Organic seston concentration, NH<sub>4</sub>: Ammonium, PO<sub>4</sub>: Phosphate, NO<sub>2</sub>: Nitrite, Chla: Chlorophyll *a* concentrations, Pheo:  
863 Pheopigment concentrations. Logarithmic transformations were applied to all data. The coefficient of determination (adjusted r<sup>2</sup>) was corrected  
864 according to the number of variables used in the regression. Copepods were analysed only at Arcachon and taken into account in stepwise regression  
865 analysis, but their inclusion does not interfere with regression results except for HNF in winter. Bold parameters are discussed in the text.  
866

		Multiple regression equations	r <sup>2</sup> adjusted	n
Marennes	Annual	log BA=2,72+0,02T°w***-0,48logSyn***+0,23logPico***+0,2logNano***+ <b>0,39logVA***</b> +0,013S%**+0,09logHNF*	90.70	84
		log VA=6,18+0,42logBA***-0,007S%*-0,003coef***+0,31logChla***-0,14logCil***- <b>0,116logPico***</b> -0,22%HNA**	71.02	84
		log HNF=-5,23+0,86logpH***+0,125logDiat**	23.68	84
		log Cil=1,19+0,46logChla***+0,44logNano***+0,11logDiat**	60.15	84
	Winter	log BA=2,02+0,02T°w***+ <b>0,5logVA***</b> +0,002coef***+ <b>0,09logHNF**</b>	81.21	40
		log VA=4,35+0,68log BA***-0,004coef***-0,28logSyn**+0,14logPheo*	77.31	40
		log HNF=-8,16+1,23logpH***-0,3logSeston Org*+0,17logDiat**	47.01	40
		log Cil=7,45+1,27logChla***-0,58logVA**+0,41logPheo**	47.87	40
	Summer	log BA=2,94+0,32logNano***+ <b>0,17logNH<sub>4</sub>**</b> - <b>0,19logNO<sub>2</sub>**</b> -0,38logSyn***+0,2logPico***+ <b>0,41logVA**</b> +0,11logchla*	74.8	44
log VA=7,61-0,003coef**+0,2logchla**+0,11logNH <sub>4</sub> *		27.21	44	
log HNF=..... log Cil=0,07+0,52logchla***+1,03logNano***-0,04T°w***+0,07logDino*		71.64	44	
Arcachon	Annual	log BA= -2,16+0,55log VA***+0,52logPico***+0,24logSyn***	94.11	31
		log VA= 2,36+1,38log BA***-0,73logSyn***- <b>0,46logPico**</b> -0,19logDino**+0,03T°w**+0,01S%*	92.83	31
		log HNF=18,19+0,22logCrypto***-0,9logVA***-1,04logCil***+1,94logSeston Org***-0,37logNH <sub>4</sub> *	84.16	31
		log Cil= 1,36+1,29logSeston Org***+1,11%HNA**+0,74logPico***-0,4logPO <sub>4</sub> ***+0,13logDino**	97.38	31
	Winter	log BA= 0,97+ <b>0,44logVA***</b> +0,99logANF***- <b>0,38logHNF**</b>	91.04	14
		log VA= 8,48-0,52logDino***	64.67	14
		log HNF=15,47-2,1logNano***- <b>0,49logCil***</b> +0,28logCop**+0,3logPO <sub>4</sub> *	94.96	14
		log Cil= -3,09+1,61logSyn***	82.23	14
	Summer	log BA= 2,47- <b>0,51logNH<sub>4</sub>***</b> + <b>0,57logVA***</b> + <b>0,33logPO<sub>4</sub>***</b>	95.86	17
log VA= 2,93- <b>0,14logHNF***</b> +0,75logChla***+0,76logBA***-0,22logSyn**		96.71	17	
log HNF= -14,53+0,4logCrypto***-0,55logDiat***+0,56S%*-0,61logPheo*		92.83	17	
log Cil= 15,49+1,58logSeston Org***-0,24S%***+0,2logVA**+0,53logNO <sub>2</sub> *		98.16	17	

\*\*\*p<0.001 \*\*p<0.01 \*p<0.05

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**Table 3.** Description of treatments used in batch culture experiments, with abbreviations employed in the text.

Water category	Organisms	Treatment	Abbreviation
<0.8µm	Bacteria Virus Picophytoeukaryotes	Control	0.8µ-Tr
		Virus enriched	Enriched-0.8µ-Tr
<3µm	+ Small nanoflagellates	Control	3µ-Tr
		Virus enriched	Enriched-3µ-Tr
<20µm	+ Large flagellates	Control	20µ-Tr
		Virus enriched	Enriched-20µ-Tr

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**Table 4.** Definitions of the characteristics of the four trophic models defined by Legendre and Rassoulzadegan (1995) and according to Rodriguez et al. (2000) and Mousseau et al. (2001). Arrows describe the abundance dynamics of the biological compartments (increasing, decreasing or fluctuating). \*\* Major parameters taken into account for the definition of trophic periods; \* secondary parameters. HNF: unpigmented nanoflagellates.

Trophic model	Large phytoplankton (>10µm)**	Small phytoplankton (<10µm)**	Bacteria**	Virus*	HNF*	Ciliates*
Herbivorous food web	↗	↘	↘	↔	↔	↗
Multivorous food web	↗	↗	↗	↗	↗	↗
Microbial food web	↘	↗	↗	↔	↗	↗
Microbial loop	↘	↘	↗	↗	↗	↔

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**Table S1.** Mean, minimum and maximum values of the abiotic and chlorophyll *a* parameters, with dates, at Marennes Bay (4 inner stations: A, B, O, Br and one riverine station: C). C was analysed separately because of the significant differences compared to the four other stations ( $H_0$  rejected in a Tukey multiple comparison test). The seasons were defined based on the clustering of stations using PCA. Winter season: January to 5 April and November-December 2006. The remainder of the year was considered as the summer season. Runoff data were supplied by DDE-Charente Maritime/HYDRO-MEDD/DE for the Charente River.

Marennes	Winter			Summer		
	Mean	Min/date	Max/date	Mean	Min/date	Max/date
Water temperature (°C)						
A,B,O,Br	9.19	5.1/1Mar.	14.5/28 Nov.	18.74	13.3/2 May	24.7/26 Jul.
C	8.59	4.8/7 Feb.	12.9/28 Nov.	19.67	13.6/2 May	24.8/26 Jul.
Salinity (PSU)						
A,B,O,Br	31.96	28.3/4 Apr.	34.3/7 Nov.	33.86	31/25 Apr.	35.3/24 Aug.
C	20.61	10.4/1 Mar.	29.8/24 Jan.	28.2	12.7/25 Apr.	33.9/1 Aug.
Nitrate (µM)						
A,B,O,Br	42.40	12.09/12 Dec.	97.98/28 Nov.	15.12	0.53/1 Aug.	78.17/25 Apr.
C	90.76	46.95/7 Nov.	192.9/12 Dec.	47.46	6.65/1 Aug.	167.5/25 Apr.
Ammonium (µM)						
A,B,O,Br	7.16	0.01/12 Dec.	68.62/28 Nov.	2.43	0.35/25 Apr.	18.85/24 Aug.
C	13.07	1.15/18 Jan.	68.83/12 Dec.	2.66	0.41/14 Jun.	7.4/25 Apr.
Phosphate (µM)						
A,B,O,Br	0.97	0.5/5 Apr.	3.04/1 Mar.	0.48	0.01/2 May	1.22/18 Sep.
C	1.25	0.77/12 Dec.	1.61/28 Nov.	1.70	0.39/4 Jul.	3.8/2 May
Silicate (µM)						
A,B,O,Br	27.74	11.35/18 Jan.	94.28/12 Dec.	13.97	4.19/2 May	56.43/26 Jul.
C	39.14	27.03/24 Jan.	58.09/28 Nov.	31.97	18.3/2 May	60.45/18 Sep.
Chl <i>a</i> (µg.l <sup>-1</sup> )						
A,B,O,Br	1.18	0.34/7 Feb.	8.31/1 Mar.	3.8	1.03/18 Sep.	16.78/2 May
C	3.58	0.43/24 Jan.	15.53/7 Nov.	4.34	1.35/30 Oct.	13.84/2 May
Total seston (mg.l <sup>-1</sup> )						
A,B,O,Br	44.16	9.54/24 Jan.	163.34/7 Nov.	16.24	4.8/5 Jun.	134.6/24 Aug.
C	1637.9	18.31/7 Feb.	8820.5/1 Mar.	57.92	12.38/5 Jun.	263.5/24 Aug.
Charente runoff (m <sup>3</sup> .s <sup>-1</sup> )	104.19	24.50/16 Nov.	380/10 Mar.	29.46	9.83/8 Sep.	71.2/25 Apr.

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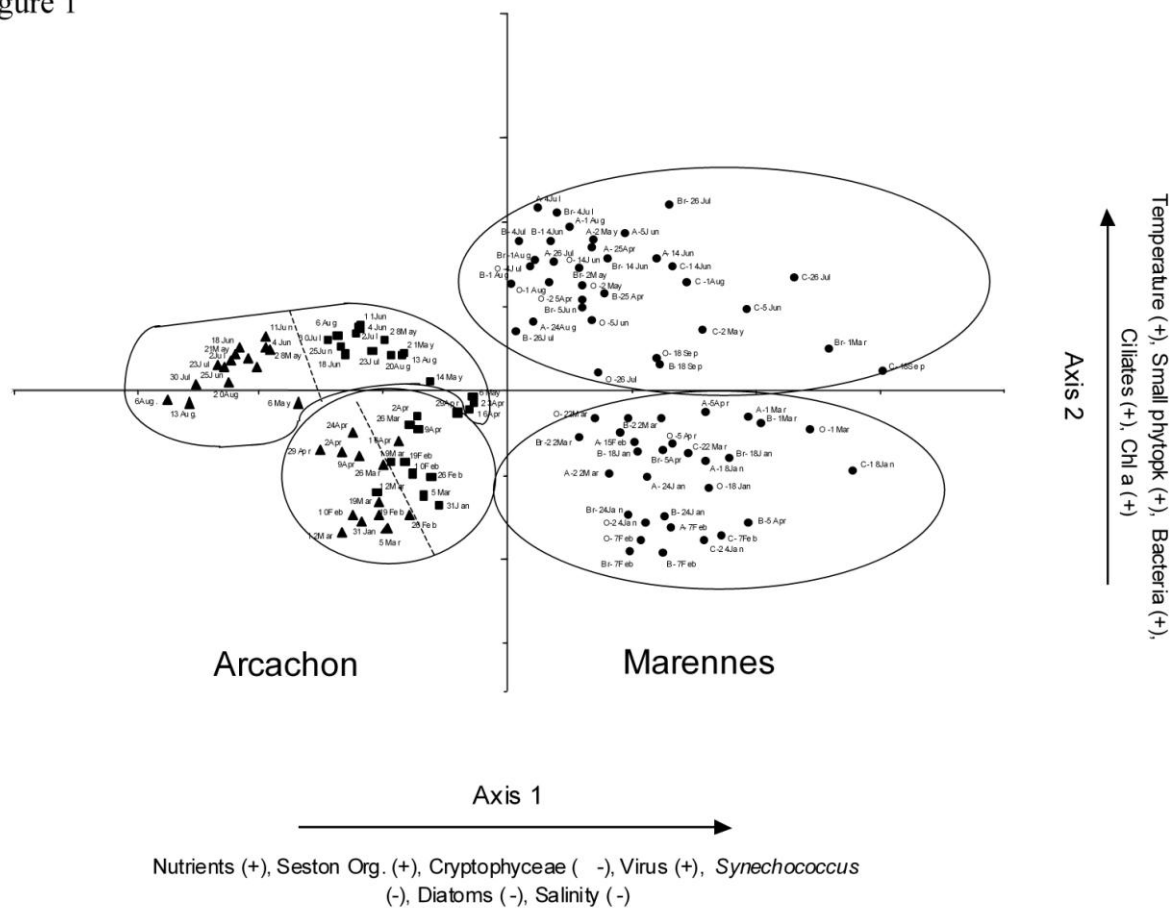
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**Table S2.** Mean, minimum and maximum values of the abiotic and chlorophyll *a* parameters with date occurrence at Arcachon Bay (B13 and Comprian stations). The seasons were defined based on the results of PCA clustering temporally the sampling stations; winter season from January to the end of April 2005. The rest of the year was considered as the summer season. Runoff data were supplied by DIREN-Aquitaine/HYDRO-MEDD/DE for Leyre River

Arcachon	Winter			Summer		
	Mean	Min/date	Max/date	Mean	Min/date	Max/date
Water temperature (°C)						
B13	10.30	7.4/5Mar.	14.8/29 Apr.	18.04	14.27/14 May	21.07/23 Jul.
Comprian	10.01	5.4/5 Mar.	16.42/29 Apr.	20.72	16.85/14 May	22.92/16 Jul.
Salinity (PSU)						
B13	34.26	24.02/29 Apr.	34.55/9 Apr.	34.49	32.3/16 Jul.	35.4/2 Jul.
Comprian	31.06	30.15/10 Feb.	32/9 Apr.	33.5	31.4/6 May.	35/30 Aug.
Nitrate (µM)						
B13	5	0.77/29 Apr.	11.21/19 Feb.	0.27	0.19/23 Jul.	0.48/6 Ma.
Comprian	8.19	2/2 Apr.	15.51/31 Jan.	0.93	0.26/16 Jul.	4.99/6 May
Ammonium (µM)						
B13	0.93	0.12/29 Apr.	4.71/31 Jan.	0.15	0.03/14 May	0.59/30 Aug.
Comprian	1.98	0.59/12 Mar.	6.46/31 Jan.	1.15	0.42/16 Jul.	2.38/30 Aug.
Phosphate (µM)						
B13	0.76	0.37/29 Apr.	2.34/26 Mar.	0.27	0.18/30 Aug.	0.36/6 May
Comprian	0.59	0.28/10 Feb.	1.8/26 Mar.	0.4	0.27/9 Jul.	0.82/13 Aug.
Silicate (µM)						
B13	4.65	0.82/9 Apr.	7.10/23 Jan.	3.6	1.31/20 Aug.	11.11/25 Jun.
Comprian	13.96	6.59/2 Apr.	21.93/31 Jan.	10.69	5.75/30 Aug.	17.78/25 Jun.
Chl <i>a</i> (µg.l <sup>-1</sup> )						
B13	0.95	0.44/12 Mar.	1.61/2 Apr.	0.77	0/30 Aug.	1.55/28 May
Comprian	1.09	0.6/5 Mar.	1.9/2 Apr.	1.37	0.72/18 Jun.	2.32/4 Jun.
Total seston (mg.l <sup>-1</sup> )						
B13	34.64	5.59/2 Apr.	216.2/23 Jan.	0.765	0.470/6 May	1.15/18 Jun.
Comprian	33.74	6.44/19 Mar.	208.7/23 Jan.	0.920	0.56/30 Aug.	1.36/9 Jul.
Leyre runoff (m3.s <sup>-1</sup> )	13.46	9.69/26 Mar.	22.8/27 Apr.	6.44	4.02/25 Aug.	16.5/1 May

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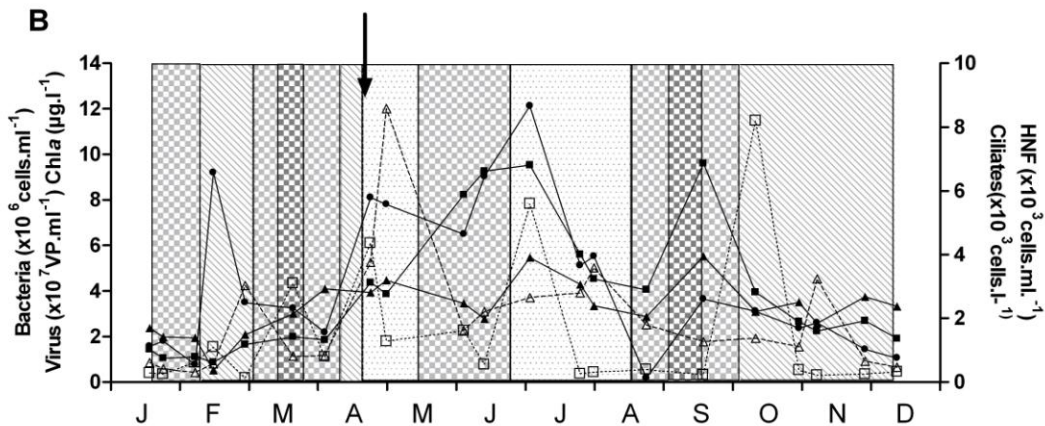
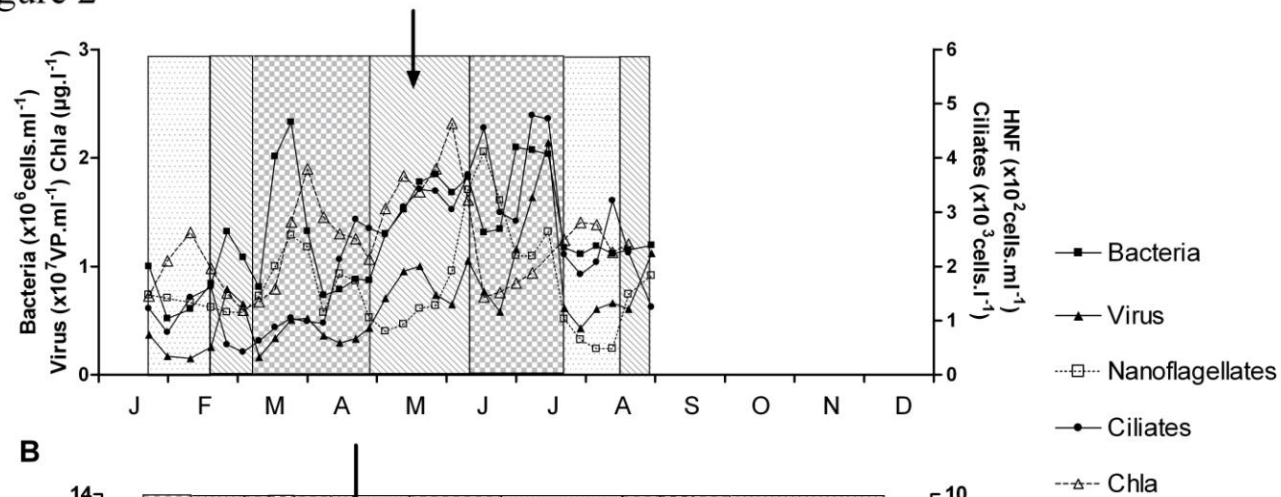
Figure 1



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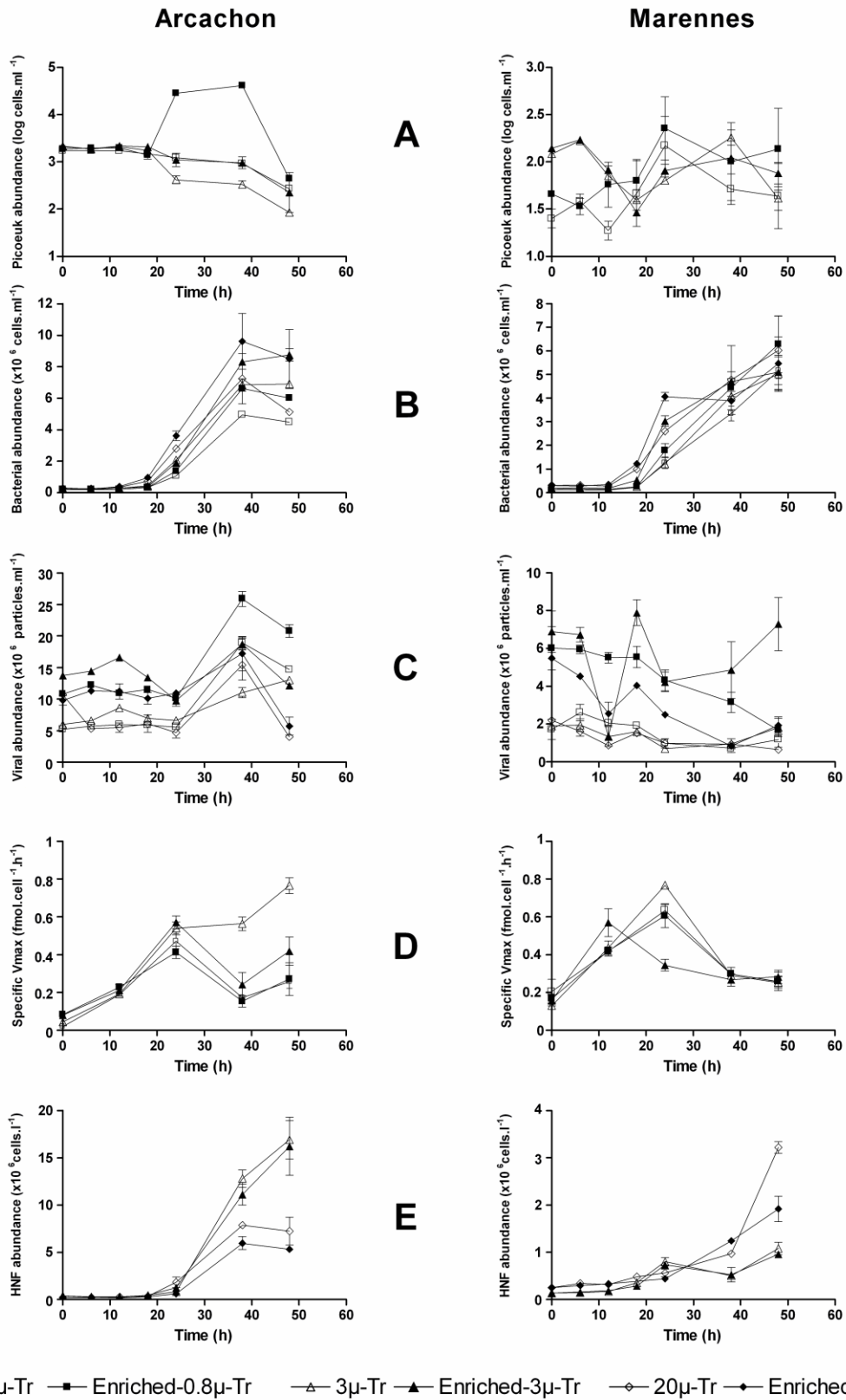
**Fig. 1.** Ordination by principal component analysis (PCA) of the basin stations obtained from microbiological, physical and chemical log transformed data in Arcachon (January to September 2005; ▲ B13, ■ Comprian, with sampling date) and Marennes-Oléron Bay (2006; ● with sampling stations and date). Arrows parallel to each axis: structuring variables. Ellipses: clusters based on hierarchical ascendant classification analysis (HAC) performed with coordinates of the station plots (straight and dotted lines: first and second discriminant in HAC, respectively).

**A**  
Figure 2



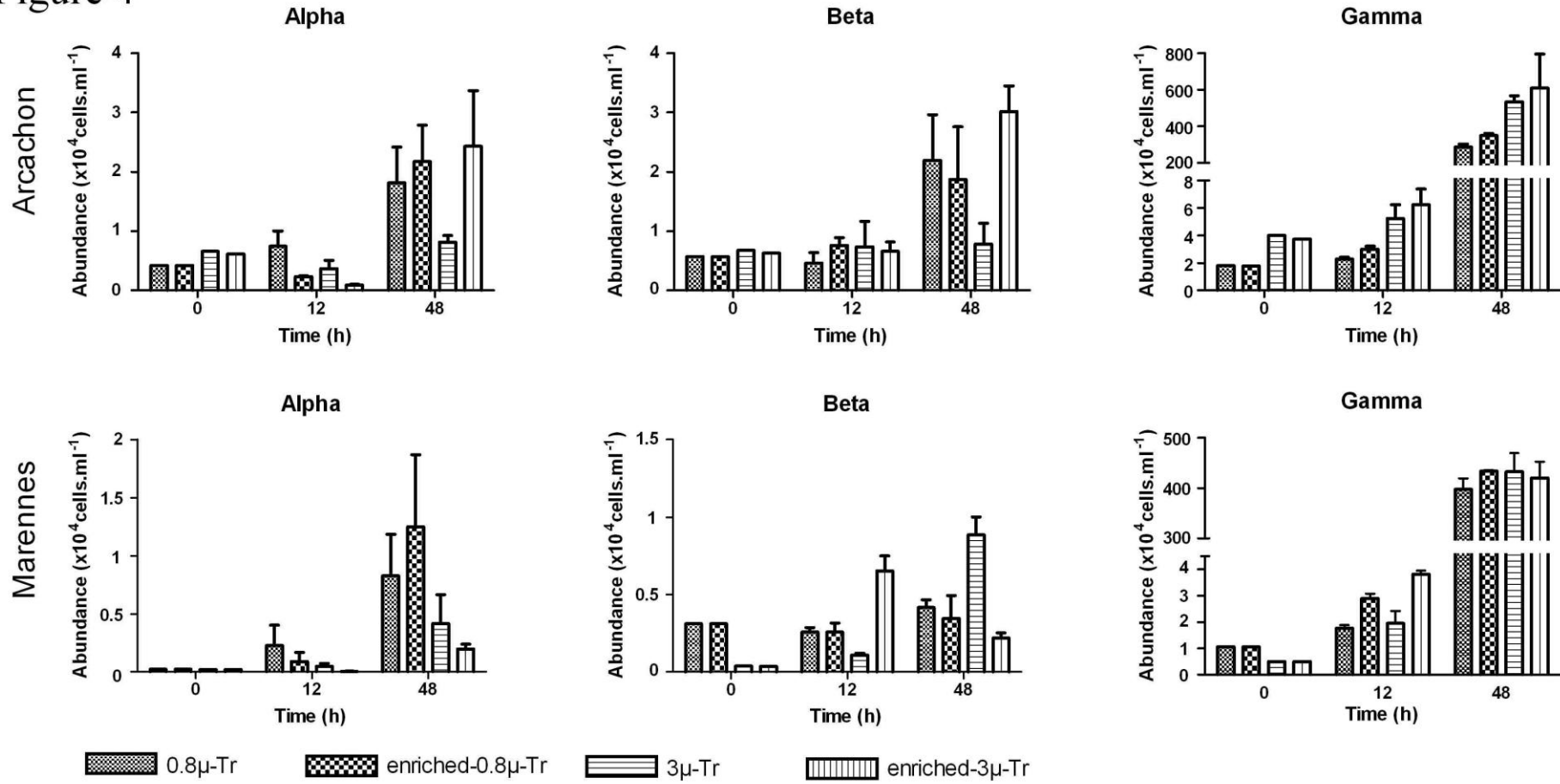
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**Fig. 2.** Temporal dynamics of bacteria ( $\blacktriangle$ ), viruses ( $\blacksquare$ ), nanoflagellates ( $\square$ ), ciliates ( $\times$ ) abundance and chlorophyll *a* ( $\Delta$ ) concentration in the 2 study sites, Arcachon in 2005 (A: Comprion station) and Marennes in 2006 (B: Mean of the 5 stations). The trophic periods are represented by different background patterns:  $\dots$  Herbivorous food web;  $\diagup$  Multivorous food web;  $\checkmark$  Microbial food web;  $\boxtimes$  Microbial loop. Arrows indicate the *in vitro* experiment periods.



**Fig. 3.** Time course of the logarithmic abundance of picophytoeukaryotes (A), abundance of bacteria (B), viruses (C), heterotrophic nanoflagellates (HNF) (E) and specific aminopeptidase bacterial activity (D) in Arcachon and Marenes experiments. Means  $\pm$  SD of triplicate incubations for each treatment.

Figure 4



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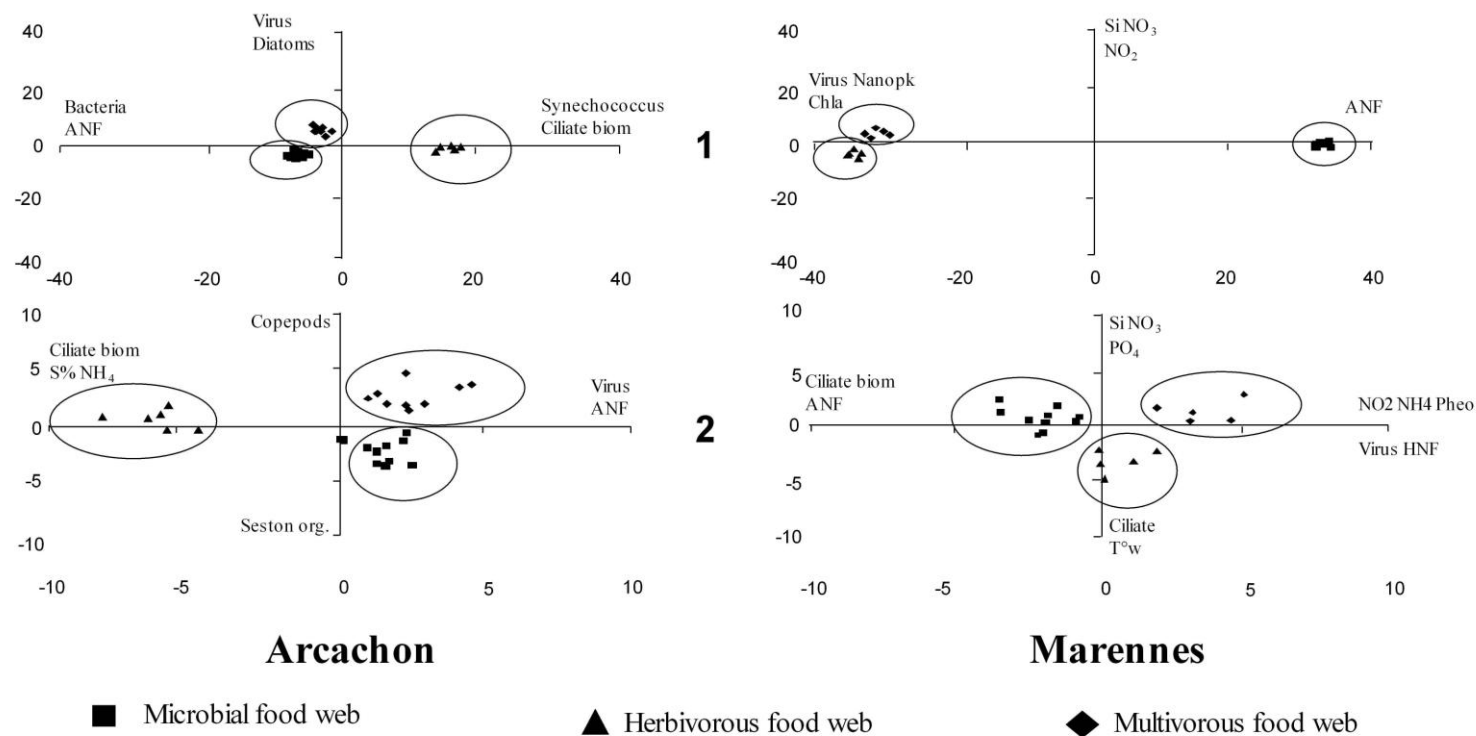
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**Fig. 4.** Bacterial community composition based on FISH analysis: dynamics of Alpha-, Beta- and Gamma-proteobacteria in different treatments of Arcachon and Marennes experiments. Gamma abundance at T48 is read on the right axis of each graph. Means ± SE of triplicate incubations for each treatment.





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943 **Fig. S1.** Ordination by factorial discriminant analysis (FDA) of samples from Arcachon (Comprian station) and Marennes (mean of the 5 stations).  
944 FDA generated from microbiological, physical and chemical data (log transformed) and using an empirical trophic model as a criterion variable (■, ▲,  
945 ◆): (1) with all the parameters and (2) excluding the principal factors used for the definition of trophic groups (large and small phytoplankton and  
946 bacteria abundance). Samples are clustered according to the trophic pattern. The microbial loop class was combined with the microbial food web class  
947 because few samples representing the former were found in Marennes and it was absent in Arcachon. Independent variables: salinity, water  
948 temperature, silicate, phosphate, ammonium, nitrate, nitrite, organic seston, pheopigment and chlorophyll *a* concentrations, abundance of viruses,  
949 bacteria, autotrophic nanoflagellates, heterotrophic nanoflagellates, ciliates, picoplankton, nanoplankton, *Synechococcus*, diatoms and Dinophyceae,  
950 biomass of ciliates and bacteria, copepods. Structuring variables are annotated along each axis: S%: salinity, ANF: Autotrophic nanoflagellates, Ciliate  
951 biom: Biomass of ciliates, Chla: Chlorophyll *a* concentration, Picopk: Picoplankton abundance, Nanopk: Nanoplankton abundance, Si: Silicate, NO<sub>2</sub>:  
952 Nitrite, NO<sub>3</sub>: Nitrate, NH<sub>4</sub>: Ammonium, PO<sub>4</sub>: Phosphate, Seston org.: Organic seston, Pheo: Pheopigment concentration, T<sup>°</sup>w: water temperature.

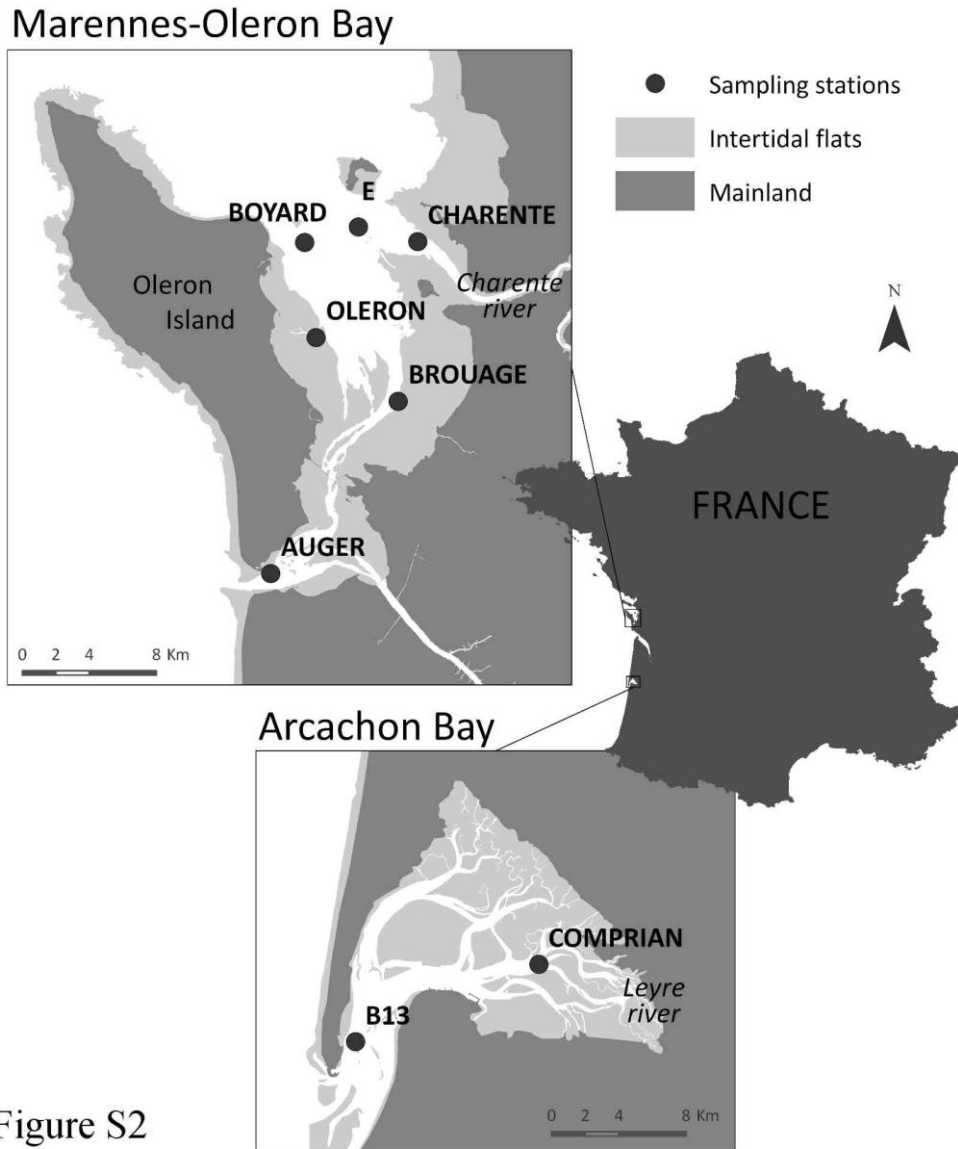


Figure S2

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**Fig. S2.** Map of the 2 study sites, Marennes-Oléron Bay and Arcachon Bay, Atlantic coast, France, showing the locations of the *in situ* sampling stations: Marennes Bay, stations Boyard (45°58'43.73''N, 1°12'30.47''W), Charente (45°58'54.94''N, 1°07'17.28''W), Oléron (45°55'41.47''N, 1°11'47.1''W), Brouage (°53'45.58''N, 1°07'52.15''W) and Auger (45°48'02.3''N, 1°13'22.7''W). Arcachon Bay, stations B13 (44°36'54.98''N, 1°14'4.15''W) and Comprian (44°40'22.8''N, 1°04'38.1''W). Location of the sampling stations for *in vitro* experiments: in Marennes Bay, station E (45°59'18.7''N, 1°10'0.69''W), in Arcachon Bay, station Comprian.