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3 **Viral infection of prokaryotic plankton during early formation of the**
4 **North West Atlantic Deep Water**

5

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20

21 **ABSTRACT:** Viral abundance was assessed in different water masses of the NW Atlantic, and the
22 development of viral abundance, lytic viral infection and lysogeny was followed for the first ca.
23 **5000 km (corresponding to ca. 50 yr in the oceanic conveyor belt)** of the western branch of the
24 North Atlantic Deep Water (NADW). Viral abundance was significantly higher in the 100 m layer
25 than in the NADW (2400–2700 m depth) and the Denmark Strait Overflow Water (2400–3600 m
26 depth). The virus-to-prokaryote ratio (VPR) increased with depth, ranging from 32–43 for different
27 water masses of the bathypelagic ocean, thus corroborating the enigma of high viral abundance in
28 the dark ocean. The O₂-minimum layer (250–600 m) also showed high viral abundance and VPRs.
29 Viral abundance, a viral subgroup and VPRs decreased in a non-linear form with distance from the
30 NADW origin. Viral production (range: 0.2–2.4 × 10⁷ viruses l⁻¹) and the fraction of lytically

31 infected cells (range: 1–22%) decreased with increasing distance from the formation site of the
32 NADW. Conservative estimations of virus-mediated mortality of prokaryotes in the NADW
33 averaged $20 \pm 12\%$. The fraction of the prokaryotic community with lysogens (i.e. harboring a
34 functional viral DNA) in the NADW averaged $21 \pm 14\%$. Hence, we conclude that (1) viral
35 abundance and subgroups differ between water masses, (2) virus-mediated mortality of prokaryotes
36 as well as lysogeny are significant in the dark ocean and (3) the lysogenic life strategy becomes
37 more important than the lytic life style during the early formation of the NADW.

38 KEY WORDS: NADW · Thermohaline circulation · Dark ocean · Viral production · Lysogeny ·
39 Microorganisms

40 1. INTRODUCTION

41 It is now well accepted that viruses represent the most abundant ‘life forms’ in the ocean and
42 that viral lysis is a major mortality factor for marine microorganisms in the upper ocean (e.g.
43 (Wommack & Colwell 2000, Weinbauer 2004, Winter et al. 2010, Zimmerman et al. 2020). Lysis
44 not only causes cell death but also releases the cell contents as dissolved organic matter (DOM) and
45 converts cell walls into small detritus; this viral shunt plays an important role in the cycling of
46 carbon and nutrients (Gobler et al. 1997, Wilhelm & Suttle 1999, Brussaard et al. 2008, Weinbauer
47 et al. 2009b) and in carbon export by the biological pump (Weinbauer et al. 2009a, Yamada et al.
48 2018).

49 During the last 1–2 decades, viral ecology of the dark ocean has been increasingly studied.
50 Data sets are available on viral abundance (VA) and production (VP) in the water column of the
51 dark realm of the Atlantic Ocean (Parada et al. 2007, De Corte et al. 2010, 2012, 2016, Muck et al.
52 2014, Winter et al. 2018), Pacific and Southern Ocean (Li et al. 2014, Yang et al. 2014),
53 Mediterranean Sea (Winter et al. 2009, Umani et al. 2010) and from a circumnavigation expedition
54 (Lara et al. 2017). Some of these studies reported that prokaryotic abundance (PA) decreased faster
55 with depth than VA, thus resulting in a high virus-to-prokaryote ratio (VPR) in the bathypelagic and
56 abyssopelagic ocean; however, there are also exceptions (Winter et al. 2009, Lara et al. 2017). This
57 presents an enigma, since host abundances are 1–2 orders of magnitude lower in deep than in
58 surface waters, which should—according to theory—result in a reduced contact rate between
59 viruses and hosts and thus in reduced viral infection and production (Murray & Jackson 1992).
60 However, it has been demonstrated that lytic VP is a major source of prokaryotic mortality in the
61 dark ocean. Data on viral production and virus-mediated mortality in the dark ocean are available
62 for the Chukchi Sea (Steward et al. 1996), Mediterranean Sea (Weinbauer et al. 2003, Winter et al.

63 2009, Umani et al. 2010), Atlantic Ocean (Parada et al. 2007, De Corte et al. 2010, 2012, Muck et
64 al. 2014) and Pacific Ocean (Li et al. 2014, Yang et al. 2014).

65 Lysogeny, i.e. the phenomenon that prokaryotic cells can harbour a provirus (viral DNA)
66 which can be induced by specific environmental conditions, has also been studied in the dark ocean
67 (Weinbauer et al. 2003, De Corte et al. 2010, 2012). It is believed that lysogeny is established when
68 the encounter rate between phages and host cells is low or when viral decay rates are high, i.e. in
69 conditions unfavourable to hosts (e.g. Stewart & Levin 1984, Weinbauer 2004). Using isolates, it
70 has been argued that a high host density destabilizes the interaction between a lytic phage and its
71 host (Bohannan & Lenski 1997). Therefore, development of lysogeny would stabilize this
72 interaction and support the survival of the phage line (Williams 1994). In this case, lysogeny might
73 also be beneficial in high host-density environments (Weinbauer 2004). Indeed, it has been
74 suggested that lysogeny can dominate when host abundance and production is high, i.e. in
75 conditions favourable for hosts ('piggyback-the-winner' model; Knowles et al. 2016). Metagenomic
76 studies suggest that provirus gene induction, and thus lysogeny, is the predominant life strategy in
77 the deep sea (Williamson et al. 2008, Mizuno et al. 2016). Some studies have reported that lysogeny
78 and inducible lysogenic VP typically increase with water depth compared to lytic VP; however,
79 other studies have also reported the inverse trend. The inducing agents of lysogenic bacteria are not
80 known for the dark ocean but it has been suggested that mixing of water masses can cause provirus
81 induction (Winter et al. 2018).

82 Depth-related variations in prokaryotic biomass and production have been summarized (e.g.
83 Nagata et al. 2000, Arístegui et al. 2009). In contrast to such depth trends, the functioning of the
84 global ocean is primarily explained by the lateral transport of physically distinct water masses
85 (thermohaline circulation) (Broecker 1997). Thermohaline circulation begins in the Greenland–
86 Iceland–Norwegian (GIN) Sea. Differences in prokaryotic activity and community composition
87 were investigated in distinct water masses of this North Atlantic Deep Water (NADW) during
88 several cruises (Reinthal et al. 2006, Teira et al. 2006, Agogué et al. 2011). Here, we investigated
89 VA and distinct viral groups as assessed by flow cytometry in the different water masses and
90 followed the development of VA, VP, lytic viral infection and lysogeny in the western branch of the
91 NADW during the TRNSAT-II cruise. The water mass was sampled from close to its formation for
92 about 5500 km, thus covering approximately the first 50 yr of the NADW in the oceanic conveyor
93 belt system.

94 2. MATERIALS AND METHODS

95 2.1. Study site and sampling

96 The western branch of the NADW was followed with the R/V 'Pelagia' from near its source
97 of origin in the GIN Sea for over ca. 5000 km (Fig. 1). The TRANSAT-II cruise (May 2003)
98 followed a track from 62.5° N, 30.3° W to 37.7° N, 69.7° W in the western basin of the North
99 Atlantic, covering 34 stations (Fig. 1). The distance of the stations from the origin of the NADW
100 was calculated using Ocean Data View (<http://odv.awi.de>). Water was collected with a CTD rosette
101 sampler holding twenty four 12 l no oxygen exchange (NOEX) bottles. Samples were taken from
102 100 m depth (subsurface layer [SSL]), the oxygen minimum zone and the main deep water masses
103 encountered during the cruise. The main water masses sampled were the Labrador Sea Water
104 (LSW), the NADW and the Denmark Strait Overflow Water (DSOW). These specific water masses
105 were identified based on their temperature and salinity characteristics (see Table 1) and their
106 oxygen concentrations, using a Seabird SBE43 oxygen sensor mounted on the CTD frame. For
107 more details of the sampling and water mass characterization, see Reinthaler et al. (2006) and Teira
108 et al. (2006). From these water masses, seawater samples were collected for physical–chemical
109 parameters, PA, VA and VP and to estimate lytic and lysogenic infection.

110 2.2. Methods for data used from previous publications

111 The following data were obtained from previous publications on the TRANSAT-II cruise.
112 For details and references see Reinthaler et al. (2006) and Teira et al. (2006). Briefly, apparent
113 oxygen utilization (AOU) was calculated as the difference between the saturation oxygen
114 concentration and the observed oxygen concentration. The concentrations of inorganic nutrients
115 (NH₄, NO₃, NO₂ and PO₄) were determined immediately after sample collection and gentle
116 filtration through 0.2 mm filters (Acrodisc; Gelman Science) in a TRAACS autoanalyzer system.
117 NH₄ was detected with the indo-phenol blue method (pH 10.5) at 630 nm. NO₂ was determined
118 after diazotation with sulfanilamide and N-(1-naphtyl)-ethylene diammonium-dichloride as the
119 reddish-purple dye complex at 540 nm. NO₃ was reduced in a copper cadmium coil to NO₂ (with
120 imidazole as a buffer) and then measured as NO₂. PO₄ was determined via the molybdenum blue
121 complex at 880 nm.

122 For enumeration of heterotrophic prokaryotes, samples (1 ml) of unfiltered seawater were
123 fixed with 37% 0.2 mm filtered (Acrodisc; Gelman) formaldehyde (2% final concentration), stained
124 with 0.5 ml of SYBR Green I (Molecular Probes) at room temperature in the dark for 15 min and
125 subsequently analyzed on a FACSCalibur flow cytometer (BD Biosciences). Counts were
126 performed with an argon laser at 488 nm set at an energy output of 15 mW. Prokaryotic cells were
127 enumerated according to their right-angle light scatter and green fluorescence measured at 530 nm.

128 Prokaryotic heterotrophic production (PHP) in seawater was measured by ^3H -leucine
129 incorporation (specific activity: 595.7 3 1010 Bq mmol^{-1} ; final concentration: 10 nmol l^{-1}). Two
130 10–40 ml samples and 1 blank were incubated in the dark. The blank was fixed with concentrated
131 0.2 mm filtered formaldehyde (4% final concentration, v/v) 10 min prior to adding the tracer. After
132 incubating the samples and the blank at *in situ* temperature for 4–12 h, depending on the expected
133 activity, the samples were fixed with formaldehyde (4% final concentration), filtered onto 0.2 mm
134 nitrocellulose filters (Millipore HA; 25 mm diameter) and rinsed twice with 5 ml ice-cold 5%
135 trichloroacetic acid (Sigma Chemicals) for 5 min. The filters were dissolved in 1 ml ethylacetate,
136 and after 10 min, 8 ml of scintillation cocktail (Insta-Gel Plus; Canberra Packard) was added. The
137 radioactivity incorporated into cells was counted in a liquid scintillation counter (Model 1212; LKB
138 Wallac). Leucine incorporated into prokaryotic biomass was converted to carbon production using
139 the theoretical conversion factor of 3.1 kg C mol^{-1} Leu, assuming a two-fold isotope dilution.

140 2.3. Enumeration of viruses

141 Water samples for viral enumeration were preserved with glutaraldehyde (0.5% final
142 concentration) at 4°C for 30 min, then flash-frozen in liquid nitrogen and stored at –80°C until
143 analysis. Virus samples were diluted 20-fold in autoclaved and 0.2 μm prefiltered TE buffer (10
144 mmol l^{-1} Tris, 1 mmol l^{-1} EDTA, pH 8.0) and stained with SYBR Green I (Molecular Probes) (at a
145 20000-fold dilution of the stock solution) in an 80°C water bath for 10 min before counting. Viruses
146 were detected by their signatures in a side-scatter-versus-green-fluorescence (530 nm wavelength,
147 fluorescence channel 1 of the instrument) plot and counted by flow cytometry (FACSCalibur; BD
148 Biosciences) following the protocol of Brussaard et al. (2010). Data analysis was performed using
149 BD Cell Quest Pro software version 4.0.2 (BD Biosciences). Viral subgroups V1, V2 and V3 were
150 distinguished by increasing fluorescence intensity with settings for the different subgroups that were
151 identical for all analyzed samples. The difference between replicates was typically better than 10%.

152 2.4. Burst size

153 To assess *in situ* burst size (BS; i.e. the number of viruses released upon cell lysis), 50 ml of
154 the prokaryotic concentrates (see below) were preserved in glutaraldehyde (0.5% final
155 concentration), kept briefly at 4°C and then stored at –80°C until analysis. Prokaryotic cells in
156 thawed samples were collected by centrifugation onto formvar-coated transmission electron
157 microscope (TEM) grids (copper, 400 mesh size) and stained with uranyl acetate (Weinbauer &
158 Suttle 1999). Duplicate grids were used for each sample. The minimum BS (BS_{min}) was estimated
159 as the average from >20 visibly infected cells grid^{-1} . This number is a conservative estimate

160 because viruses could still be assembled in the cells; therefore, a conversion was used to calculate
161 maximum BS (BS_{\max}): $BS_{\max} = 1.41 \times BS_{\min} + 0.87$ (Parada et al. 2006).

162 2.5. VP and infection of prokaryotic plankton

163 VP, the fraction of infected cells (FIC) and the fraction of lysogenic cells (FLC) were
164 estimated with a dilution technique (Wilhelm et al. 2002) using a modification described elsewhere
165 (virus-reduction approach [VRA]: Weinbauer et al. 2002, 2010). Large water samples (150–200 l)
166 were filtered through 0.8 mm pore-size polycarbonate filters (142 mm diameter; Millipore) and
167 prokaryotes were concentrated using a Pellicon (Millipore) tangential flow filtration system
168 equipped with a 0.2 μm filter cartridge (Durapore; Millipore) as described in (Weinbauer et al.
169 2009b). The first 20 l of the 0.2 μm filtrate were processed with a 100 kDa cutoff polysulfone
170 cartridge (Prep-Scale/TFF; Millipore: 0.23 m^2 nominal filter area, operated by a peristaltic pump at
171 150000 Pa) to produce virus-free water. Aliquots of the prokaryote concentrate were added to virus-
172 free water to obtain roughly *in situ* abundance assuming (based on previous findings) that half of
173 the prokaryotes were lost during the prefiltration and ultrafiltration steps. This procedure reduces
174 contact rates between viruses and hosts and thus new infection. Incubations were performed in the
175 dark at *in situ* temperature (3.0°C) in duplicate 50 ml sterile conical tubes for 24 h. Samples were
176 taken at incubation times (t) 0, 6, 12, 18 and 24 h. VP was calculated as:

$$177 \quad \text{VP} = (\text{VA}_2 - \text{VA}_1) / (t_2 - t_1) \quad (1)$$

178 where VA_1 and VA_2 are the viral abundances at incubation times t_1 and t_2 , respectively. Note that
179 individual incubations were treated separately and values at the start of incubations were not always
180 used for calculations. Rather, the lowest viral abundance served as VA_1 (Weinbauer et al. 2009b).
181 Thus, VA_1 and VA_2 are the minimum and maximum of viral abundance in the incubation. VP was
182 corrected for the changes in PA at the start of the experiment compared to *in situ* abundances.

183 Dividing the number of produced viruses by the BS yields the number of lysed cells and
184 thus gives an estimate of FIC (Weinbauer et al. 2002), which was calculated by:

$$185 \quad \text{FIC} = 100(\text{VA}_2 - \text{VA}_1) / \text{BS} / \text{PA} \quad (2)$$

186 where PA is the prokaryotic abundance at the start of the experiment (t_1). Virus-mediated mortality
187 of prokaryotes (VMMP) was either calculated as:

$$188 \quad \text{VMMP}_{\text{VP}} = 100(\text{VP} / \text{BS} / \text{PHP}) \quad (3)$$

189 or using FIC values and the model of Binder (1999) (VMMP_{FIC}).

190 The FIC treatment also served as a control in the lysogeny bioassays. To induce the lytic
191 cycle in lysogenic cells (containing a prophage), samples were treated with mitomycin C (Sigma

192 Chemicals; final concentration: 0.5 $\mu\text{g ml}^{-1}$; Paul & Weinbauer 2010). The difference in VA
193 between this treatment and the control is the number of induced viruses, which is divided by the BS
194 to estimate the number of induced cells and thus the FLC. FLC was calculated as percentage by:

$$195 \quad \text{FLC} = 100(\text{V}_{\text{AMC}} - \text{V}_{\text{AC}}) / \text{BS} / \text{PA} \quad (4)$$

196 where V_{AMC} and V_{AC} are the maximum difference in viral abundance at corresponding time points
197 in mitomycin C and control treatments, respectively. Induced VP (VP_i) was calculated analogous to
198 VP after by subtracting V_{AC} from V_{AMC} .

199 **2.6. Statistics**

200 Spearman rank correlations were used to assess the covariation of parameters, since some
201 variables did not comply with normality even after logarithmic transformation. The non-parametric
202 Kruskal-Wallis and Mann-Whitney tests were used for comparing specific parameters obtained in
203 different water masses, since normality was not always attained; $p < 0.05$ (after applying a
204 Bonferroni correction) was considered significant. To test a potential change of viral parameters
205 with distance from the GIN Sea, regressions with linear, logarithmic, exponential and power
206 functions were calculated; $p < 0.05$ was considered significant. Statistics were performed with
207 Aabel_3.

208 **3. RESULTS**

209 **3.1. Characterization of water masses**

210 Some basic physical–chemical characteristics of the main water masses sampled during the
211 study are given in Table 1. More details can be found elsewhere (Teira et al. 2006). The LSW,
212 characterized by low salinity, was clearly identifiable at depths between 700 and 2100 m, except
213 between 40 and 45° N. The NADW (2000–3000 m) was identifiable by its salinity maximum
214 (34.90–34.95) south of 60° N. The DSOW underlying the NADW, with seawater temperature
215 between 0.8 and 2.4°C and salinity < 34.90 , was detected at all stations between 45 and 65° N. A
216 local moderate oxygen minimum (ca. 30% less than in overlaying and underlying water) was
217 found between ca. 200 and 700 m depth in the southern part of the transect (from 40–50° N). Data
218 were only used when these water masses could be clearly identified.

219 **3.2. VA and PA in different water masses; depth relationships**

220 The distribution of PA is shown in Fig. 2. PA decreased with depth by ca. an order of
221 magnitude (Table 2), and this decrease was exponential (Reinthaler et al. 2006). The various deep-
222 water masses exhibited some differences in PA. PA was highest in the SSL (> 100 m depth),

223 intermediate in the oxygen minimum zone and lowest in the bathypelagic water masses. These
224 differences were significant (Kruskal-Wallis and Mann-Whitney tests, $p < 0.05$; Table 2).

225 VA (Fig. 2) showed a local maximum in the oxygen minimum zone at ca. 54° N, 47° W (ca.
226 500 m water depth) and was slightly higher close to the GIN Sea. VA decreased significantly with
227 depth (Table 3) and was, on average, highest in the SSL ($3.1 \pm 1.8 \times 10^9 \text{ l}^{-1}$) and oxygen minimum
228 zone ($2.7 \pm 2.9 \times 10^9 \text{ l}^{-1}$) and lowest in the NADW ($1.2 \pm 0.9 \times 10^9 \text{ l}^{-1}$) (Table 2). Significant
229 differences were found between the SSL and the NADW/DSOW (Kruskal-Wallis and Mann-
230 Whitney tests, $p < 0.05$); however, differences between depth layers were less pronounced than for
231 PA and were a maximum of 3.3-fold. The VPR also showed a local maximum in the oxygen
232 minimum zone at 47.6° W, 53.5° W and was also highest towards the GIN Sea. In addition, VPR
233 increased significantly with depth (Table 3). VPR was lowest in the SSL and highest in the DSOW;
234 VPR was significantly lower in the SSL than in bathypelagic waters (Kruskal-Wallis and Mann-
235 Whitney tests, $p < 0.05$; Table 2).

236 There was a tendency that %V3 (the viral subgroup with the highest fluorescence) was
237 highest in surface water, whereas %V1 was lower and %V2 was higher in the bathypelagic ocean
238 than in surface water (Fig. 3, Table 2). A local maximum of %V1 and a local minimum of %V2 and
239 %V3 was found at the oxygen minimum at 47.6° W, 53.5° W. Significant differences between some
240 water masses were found for all 3 viral flow cytometer groups (Kruskal-Wallis and Mann-Whitney
241 tests, $p < 0.05$; Table 2). Significant differences with depth were only found for %V1 and %V2
242 (Table 3).

243 Co-variation of physico-chemical and biological parameters was assessed across water
244 masses (Table 3). PA and VA increased with temperature and decreased with AOU, PO_4 and NO_3 .
245 There were positive correlations between PA, VA and PHP.

246 3.3. Viral and microbial parameters in the NADW

247 In order to assess potential changes of parameters with the formation and ageing of the
248 NADW, the distance of stations from the GIN Sea was calculated as a proxy for the length of the
249 NADW (Fig. 1). Temperature and salinity increased significantly with distance from the GIN Sea.
250 PO_4 and NO_3 concentrations increased also with distance. Oxygen concentrations decreased
251 significantly with distance, whereas AOU increased (Table 4). VA and VPR decreased significantly
252 with distance, but in a non-linear way (see also Fig. 3). The %V1 increased (from the 2 stations
253 closest to the GIN Sea) and V2 decreased significantly with distance (Table 4, Fig. 3).

254 BS was assessed at Stns 1, 13 and 31, averaging 28 ± 5 (range: 24–33 for the 3 samples)
255 after correction to BS_{max} . For VP measurements, VA in the incubations was reduced by $77 \pm 13\%$

256 compared to *in situ* VA, whereas PA was $69 \pm 16\%$ of *in situ* abundance. VP averaged 0.95 ± 0.78
257 $\times 10^4$ viruses $l^{-1} d^{-1}$ (Table 5). FIC averaged $14 \pm 7\%$, mean VMMP_{VP} was $59 \pm 52\%$ and VMMP_{FIC}
258 $20 \pm 12\%$. VP_i averaged $1.7 \pm 1.4 \times 10^7$ viruses $l^{-1} d^{-1}$, while FLC averaged $21 \pm 14\%$. VP and FIC
259 decreased with distance from the GIN Sea, whereas for VP_i and FLC no significant relationship was
260 found (Fig. 4).

261 Co-variation of parameters was also assessed within the NADW (Table 4). PA was
262 positively related to oxygen concentration and negatively related to salinity and AOU. VA was
263 negatively related to AOU, PO₄ and NO₃ concentrations and positively to oxygen.

264 4. DISCUSSION

265 The data presented here indicate that different water masses maintain specific viral
266 characteristics during their early lateral flow in the oceanic conveyor belt. Nevertheless, for the
267 NADW, successional changes with distance from the origin could be observed for VA, subgroups,
268 infection and lytic production.

269 4.1. Depth distribution of viruses

270 The decrease of VA with depth during early formation of the NADW was much less
271 pronounced than for PA (Fig. 1, Table 2). Similar trends were found for the Atlantic (Parada et al.
272 2007, De Corte et al. 2010, 2012, 2016, Muck et al. 2014, Winter et al. 2018) and the Pacific (Li et
273 al. 2014, Yang et al. 2014). Vertical transport of sinking particles is probably not always
274 responsible for the high VPRs in the dark ocean as previously suggested (Hara et al. 1996), since
275 very high VPRs were found in bathypelagic areas where sinking particle fluxes are generally low
276 (Yang et al. 2014). However, since viruses can enhance aggregate formation and export into the
277 dark ocean (i.e. viral shuttle; Peduzzi & Weinbauer 1993, Sullivan et al. 2017, Yamada et al. 2018,
278 Boeuf et al. 2019), viral lysis can also contribute to the sinking of viruses attached to aggregates.

279 Among the main causes for viral decay in the absence of sunlight are high temperatures,
280 high molecular weight DOM and microscopic (inorganic) particles (Suttle & Chen 1992, Cottrell &
281 Suttle 1995, Noble & Fuhrman 1997). One of the obvious reasons for the high abundances of
282 viruses in bathypelagic waters could be low decay due to low temperatures (Parada et al. 2007).
283 This is supported by the finding that the VPR was lower and water temperature ca. 13°C higher in
284 the bathypelagic zone of the Mediterranean Sea (Magagnini et al. 2007, Winter et al. 2009) than in
285 the Atlantic Ocean.

286 While the low DOM concentrations in the dark ocean (e.g. Aristegui et al. 2009) likely mean
287 reduced decay, large microscopic particles are plentiful (Bochdansky et al. 2010, 2016, Boeuf et al.

288 2019) and could thus be a significant cause of viral decay. However, since there is evidence that
289 organic particles (marine snow) are viral factories rather than viral traps (Weinbauer et al. 2009a,
290 Bettarel et al. 2016), the particles in the dark ocean could protect viruses against decay and even
291 foster VP. If the emerging notion holds that deep-sea prokaryotes are preferentially particle-
292 attached (e.g. DeLong et al. 2006, Baltar et al. 2009, Swan et al. 2011), these particles might be
293 hotspots of viral infection by increasing contact rates and, hence, abundance (De Corte et al. 2012).

294 It has often been assumed that there is a trade-off for prokaryotes between competition for
295 nutrients and resistance against viral infection (Thingstad 2000, Winter et al. 2010). From a fitness
296 perspective (Thingstad et al. 2014, Thingstad & Våge 2019), one could argue that—as the supply
297 with organic material is low in the deep-sea (Aristegui et al. 2009)—favouring DOM uptake
298 abilities should occur at the expense of defence against viral infection. This should result in higher
299 VP, especially when contact rates remain high in cases where the viruses and microbes are mainly
300 particle-attached (see paragraph above), and thus in a high VPR in the deep-sea.

301 There is no simple relationship between fluorescence intensity and genome size of viruses.
302 However, as viruses do not have their own metabolism, the staining intensity with dyes such as
303 SYBR Green does not vary for specific types of viruses. Therefore, changes in the relative
304 proportion of viral subgroups indicate changes of viral community composition (Brussaard et al.
305 2010). Consequently, the variation of the viral subgroups between depth layers (Table 2) suggests
306 differences in viral community composition. Such differences between viral subgroups have also
307 been found in other studies (De Corte et al. 2010, Muck et al. 2014) and were confirmed by using
308 pulsed-field gel electrophoresis (Parada et al. 2007), randomly amplified polymorphic DNA-PCR
309 (RAPD-PCR; De Corte et al. 2010, Winter & Weinbauer 2010, Muck et al. 2014) and
310 metagenomics (Mizuno et al. 2016, Winter et al. 2018, Gregory et al. 2019, Liang et al. 2019).
311 Using viral subgroups, the strongest differences were found between the SSL and bathypelagic
312 water masses, suggesting that specific viral communities are inhabiting these environments. A
313 likely reason for the differences in viral community composition is differences in host activity and
314 community structure diversity in these water masses as assessed during the same cruise (Teira et al.
315 2004, Reinthaler et al. 2006).

316 4.2. Lysogeny in the NADW

317 FLC in the NADW data ranged from 4.5–40.1%, which is similar to another study from the
318 deep ocean using the VRA approach (10.1–27.3%; Muck et al. 2014). Using a whole seawater
319 approach, FLC values were found to be highest in the bathypelagic zone of the Mediterranean Sea

320 (73.2%; Weinbauer et al. 2003). Using the VRA approach, FLC values from the NADW were
321 higher than FIC values (Fig. 4, Table 5).

322 FLC and lysogenic VP did not vary significantly with distance from the GIN Sea (Fig. 4b,d,
323 Table 5). Also, FLC and lysogenic VP did not vary significantly with PHP (Spearman rank
324 correlation, $\rho < 0.65$, $p > 0.15$). In other studies of the Atlantic Ocean, inducible VP did not change
325 (or changed little) with depth from the epipelagic to the abyssopelagic zone, whereas PA, PHP and
326 lytic VP decreased strongly with depth (De Corte et al. 2010, 2012, Muck et al. 2014).
327 Metagenomic data indicate that lysogeny is the predominant life strategy in the deep ocean
328 (Williamson et al. 2008, Mizuno et al. 2016). Thus, these data support the general idea that
329 lysogeny dominates when the encounter rate between phages and host cells is low (Stewart & Levin
330 1984, Weinbauer et al. 2003, Weinbauer 2004). However, in the Malaspina Circumnavigation
331 Experiment, Lara et al. (2017) found that lysogeny dominated in surface water and lytic VP became
332 more important in deep water, hence supporting both hypotheses, i.e. promotion of lysogeny by low
333 growth rates and low nutrient conditions ('classic' explanation) and promotion at high host
334 abundance ('piggyback-the-winner' model) (Knowles et al. 2016). This indicates that the lytic–
335 lysogenic switch is likely more complex than previously thought, which calls for further studies
336 (Lara et al. 2017). Independent of the lytic–lysogeny switch argument, all studies show that
337 lysogeny is significant in the deep sea. It has been hypothesized that marine prophages directly
338 contribute to host survival in unfavourable environments by suppressing superfluous metabolic
339 activities (Paul 2008), which could be particularly important in the carbon-limited dark ocean.

340 **4.3. VA and infection during the formation of the NADW**

341 VA, VPR, lytic VP and FIC decreased with distance from the GIN sea. Among the factors
342 which could have influenced these parameters during the early formation of the NADW are (1)
343 physical factors (temperature or mixing of the NADW with adjacent water masses), (2) sinking of
344 particles from surface water into the interior of the ocean (export of viruses or stimulation of host
345 activity) and (3) successional (i.e. internal temporal changes such as changes in community
346 composition or resistance).

347 VA decreased in the NADW and temperature increased with distance from its formation
348 (Fig. 3, Table 4). It is possible that the ca. 50 yr transport into warming water resulted in an
349 increased decay and contributed to losses of viruses. The increase in temperature and salinity in the
350 NADW with distance from its formation (Table 4) is caused by mixing with adjacent water masses
351 such as the overlying LSW, which is warmer and lower in salinity than the NADW (van Aken
352 2000a,b). Since VA was higher in the LSW than in the NADW, one would expect VA to increase

353 with distance in the NADW; however, they decreased, instead indicating that other factors were
354 more important than direct mixing processes. Mixing of deep sea water masses can cause an
355 increase in prokaryotic production and hence VP (Muck et al. 2014) e.g. by induction of lysogens
356 (Winter et al. 2018). Our data set did not allow us to evaluate this possibility for the NADW.

357 General distribution patterns of chlorophyll *a* (chl *a*) during the TRANSAT-II cruise suggest
358 a potentially decreasing sinking particle flux and thus a potentially decreasing viral export flux with
359 distance from the GIN Sea (Teira et al. 2004, Reinthaler et al. 2006). If sinking particles are a
360 source of viruses for the dark ocean, such a pattern could contribute to the finding of a decrease in
361 VA and VPR with age of the NADW (but see discussion on transport of viruses on particles in
362 Section 4.1). Release of viruses from sinking particles could for example explain local maxima of
363 viral parameters as detected in this study (Fig. 2). The decrease of VA, VPR, VP and FIC with
364 distance from the GIN Sea was not accompanied by a change in PA and PHP (Table 4). Thus, there
365 is no support for the hypothesis that sinking aggregates (transporting viruses and prokaryotes) or the
366 supply of organic matter into the NADW caused the observed viral (and prokaryotic) patterns with
367 distance from the GIN Sea.

368 Assuming a conservative prokaryotic turnover time of ca. 1 mo in the NADW (Reinthaler et
369 al. 2006) and an investigated time frame for the formation of the NADW of 50 yr, prokaryotes
370 produced ca. 600 generations of offspring. Correlation analysis indicates that (micro)organisms
371 consume oxygen and remineralize PO₄ and NO₃ during this transport (Table 4). It is possible that
372 prokaryotic community composition changed during these 600 generations. Changes in community
373 composition of hosts can affect the community composition of virioplankton (e.g. Winter et al.
374 2010). Such a mechanism could explain the finding that viral community composition, as indicated
375 by the relative abundance of viral groups, changed significantly with age of the NADW. Since the
376 BS of viruses is quite variable (Børsheim 1993), changes in the community composition to virus–
377 host systems with lower BSs could contribute to the decrease of VA and VPR with distance from
378 the GIN Sea. The few data on BS support this idea (Table 5).

379 In a 2 yr pressure incubation (corresponding to pressure at 3000 m water depth) with various
380 phage isolates and a natural virus community, it was found that small and low fluorescence viruses
381 decayed slower than larger or high fluorescence viruses (Tian et al 2020). The finding that the
382 proportion of the V1 group (low fluorescence) became more important with distance from the GIN
383 Sea compared to V2 and V3 groups (higher fluorescence) (Fig. 3b,c) could therefore be explained
384 by lower decay rates. Thus, variable decay rates between different types of viruses could change the
385 virus community and hence infection patterns.

386 Resistance against infection is a well known phenomenon from studies with isolates (Avrani
387 et al. 2012). Among the more recently detected resistance mechanisms is CRISPR (Barrangou et al.
388 2007). CRISPR is a sort of immune system for prokaryotes in the sense that it confers resistance to
389 bacterial and archaea cells against mobile genetic elements such as viruses (e.g. Barrangou et al.
390 2007, Vestergaard et al. 2008). Exposure of prokaryotes to viruses for 600 generations and
391 development of resistance is therefore another possible cause for the decrease of VA and lytic
392 infection with ageing NADW. If the resistance hypothesis holds, viral types belonging to the V2
393 group would be the loser in the arms-race with prokaryotic hosts compared to type V1, which
394 decrease in relative abundance with distance from the GIN Sea.

395 Applying the reasoning of a fitness penalty in a low-nutrient environment (see Section 4.1),
396 it can be argued that the fitness costs of resistance should increase with distance from the GIN Sea,
397 i.e. with the ageing of NADW. Hence, a strategy towards competitive traits with high susceptibility
398 to viral infection could be anticipated. However, there is no evidence that viral infection or VPR
399 increased; on the contrary, these parameters decreased with distance from the GIN Sea. Overall,
400 VPR was very high at the origin of the GIN Sea, and despite the decline with ageing of the NADW
401 it remained higher than in surface water. It is possible that the high VPR values in origin water
402 masked fitness-related trends. In this context, it is important to mention that temperature increased
403 in the NADW with distance from the GIN Sea. Alternatively, the origin water could have been
404 already characterized by conditions favouring competitive over defence traits.

405 **4.4. VP, mortality and carbon release in the NADW**

406 Lytic VP ranged from $2.2\text{--}2.5 \times 10^7 \text{ l}^{-1} \text{ d}^{-1}$. These values are slightly lower than the lytic VP
407 estimated in other bathy- and abyssopelagic environments ($3.6 \times 10^7\text{--}8.4 \times 10^9 \text{ l}^{-1} \text{ d}^{-1}$) (De Corte et
408 al. 2010 2012, Umani et al. 2010, Li et al. 2014, Muck et al. 2016, Lara et al. 2017, Winter et al.
409 2018). The FIC (0.6–22.0%) was at the lower range compared to other studies (15–143%; Muck et
410 al. 2014, Winter et al. 2018).

411 Using 2 different methods for estimating the role of viral lysis for prokaryotic mortality,
412 estimates based on VMMP_{VP} were on average 2.7 higher than estimates based on VMMP_{FIC} (Table
413 5). It is a well known but poorly understood phenomenon that different methods for estimating
414 VMMP are not always fully congruent (Winter et al. 2004, Helton et al. 2005, Winget et al. 2005,
415 Weinbauer et al. 2009b). Nevertheless, data from both methods suggest significant mortality due to
416 viral lysis in the NADW (on average 20% by VMMP_{FIC} and 59% by VMMP_{VP} , respectively).
417 Finally, viruses have been detected within cells (Weinbauer et al. 2003, this study). This finding
418 supports that of Li et al. (2014) that there is an autochthonous active virus community in the deep

419 sea. Also, endemic deep-sea virus communities have been documented by metagenomics (Winter et
420 al. 2014, 2018, Mizuno et al. 2016, Gregory et al. 2019, Liang et al. 2019).

421 Using a conversion factor of 12.4 fg cell⁻¹ for the dark ocean (Fukuda et al. 1998) and data
422 from Table 5, the carbon release by viral lysis of prokaryotes would be 8.6 ± 5.5 ng C l⁻¹ d⁻¹ using
423 VMMP_{VP} and 2.9 ± 1.4 ng C l⁻¹ d⁻¹ using VMMP_{FIC}. This is lower than the 0.03–0.69 µg C l⁻¹ d⁻¹
424 estimated by Li et al. (2014). The majority of DOM in the deep sea is characterized by low turnover
425 times and is either too recalcitrant or too diluted to be used by prokaryotes (Jiao et al. 2011, Arrieta
426 et al. 2015). Viral lysis products consist of cell contents and wall cell debris such as DNA, RNA,
427 carbohydrates, amino acids, glucosamine and diaminopimelic acid (Weinbauer et al. 1993,
428 Weinbauer & Peduzzi 1995, Middelboe & Jorgensen 2006) and are rapidly degraded, hence
429 belonging to the pool of labile DOM (Noble & Fuhrman 1999, Middelboe & Lyck 2002). This may
430 relieve the carbon limitation of the growth of deep-sea prokaryotes. Also, organic matter from cells
431 shunted into the DOM pool by viral lysis is hardly accessible to higher trophic levels, thus resulting
432 in a slower transfer of organic matter towards higher trophic levels (Fuhrman 1999). This process
433 could sustain a high prokaryotic biomass and provide an important contribution to prokaryotic
434 metabolism, allowing the system to cope with the severe organic resource limitation of deep-sea
435 ecosystems as has been demonstrated for benthic and pelagic communities (Danovaro et al. 2008,
436 Lara et al. 2017). Moreover, viral lysis may prime the biological pump and the microbial carbon
437 pump and hence carbon sequestration in the ocean, which has significant global consequences
438 (Suttle 2007, Brussaard et al. 2008, Jiao et al. 2011, Guidi et al. 2016).

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682 Table 1. Averaged water layer properties of selected physico-chemical parameters in the western North Atlantic basin. *T*: temperature; σ_t : water
 683 density. SSL: subsurface layer; O₂-min: oxygen minimum zone; LSW: Labrador Sea Water; NADW: North Atlantic Deep Water; DSOW: Denmark
 684 Strait Overflow Water. **Values in parentheses: SD**

Water mass	No. of samples	Depth (m)	Depth range (m)	<i>T</i> (°C)	σ_t (kg m ⁻³)	Oxygen ($\mu\text{mol kg}^{-1}$)
SSL	33	100	90–110	8.7 (4.74)	27.20 (0.489)	260 (38.4)
O ₂ -min	15	402	180–740	7.9 (2.39)	27.32 (0.194)	187 (51.2)
LSW	32	1324	710–2090	3.4 (0.32)	27.77 (0.031)	279 (7.3)
NADW	23	2537	1980–3250	3.0 (0.19)	27.84 (0.014)	272 (6.5)
DSOW	22	3031	1220–3870	1.9 (0.42)	27.91 (0.24)	288 (12.7)

685

686 Table. 2. Prokaryotic and viral parameters in the western North Atlantic basin. PA: prokaryotic abundance; VA: viral abundance; V1: viral subgroup 1;
 687 V2: viral subgroup 2; V3: viral subgroup 3; VPR: virus-to-prokaryote ratio. SSL: subsurface layer; O₂-min: oxygen minimum zone; LSW: Labrador
 688 Sea Water; NADW: North Atlantic Deep Water; DSOW: Denmark Strait Overflow Water. **PHP** and PA data are from [Reinthal et al. \(2006\)](#).
 689 **Numbers in parentheses: SD; letters in parentheses:** Mann-Whitney tests of pairs of water masses (levels not connected by same letter are significantly
 690 different [$p < 0.05$]).

Water mass	No. of samples	PA ($\times 10^8$ cells l ⁻¹)	VA ($\times 10^9$ particles l ⁻¹)	V1 (%)	V2 (%)	V3 (%)	VPR
SSL	33	3.58 (0.94) (A)	3.1 (1.8) (A)	73.1 (4.0) (A)	20.3 (4.1) (A)	6.5 (1.5) (A)	9.8 (5.6) (A)
O ₂ -min	15	1.27 (0.49) (B)	2.7 (2.9) (A,B)	78.3 (9.1) (A,B)	17.2 (7.8) (A)	4.5 (1.6) (B)	27.0 (38.9) (A)
LSW	32	0.50 (0.17) (C)	1.5 (0.8) (A,B)	66.3 (7.3) (B,C)	28.8 (7.5) (A)	4.8 (1.7) (B)	32.4 (21.3) (A)
NADW	25	0.30 (0.06) (C)	1.2 (0.9) (B)	69.0 (5.8) (B,C)	26.4 (5.1) (B)	4.6 (2.0) (B)	40.8 (26.5) (A,B)
DSOW	22	0.43 (0.26) (C)	2.3 (2.1) (B)	69.2 (8.1) (C)	26.1 (7.3) (B)	4.6 (1.7) (B)	42.9 (18.2) (B)
Kruskal-Wallis (p-value)		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

691

692 Table 3. Spearman rank correlations (ρ) of parameters of the entire study. Values in **bold**: $p < 0.05$; values in *italics*: $p > 0.5$. Physico-chemical and
 693 prokaryotic data are from Teira et al. (2005) and Reinthaler et al. (2006). AOU: Apparent oxygen utilization; PA: prokaryotic abundance; PHP:
 694 prokaryotic heterotrophic production; VA: viral abundance; V1: viral subgroup 1; V2: viral subgroup 2; V3: viral subgroup 3; VPR: virus-to-
 695 prokaryote ratio

	Depth	Temp	Salinity	O ₂	AOU	PO ₄	NO ₃	PHP	PA	VA	%V1	%V2	%V3
PA	-0.887	0.760	0.109	-0.059	-0.426	-0.463	-0.449	0.622					
VA	-0.508	0.411	-0.104	-0.101	-0.349	-0.314	-0.284	0.474	0.450				
%V1	-0.239	0.249	0.209	-0.216	0.078	0.096	0.097	0.235	0.076	0.390			
%V2	0.260	-0.238	-0.174	0.158	0.009	-0.026	-0.032	-0.241	-0.123	-0.438	-0.928		
%V3	-0.010	-0.060	-0.187	0.219	-0.268	-0.249	-0.245	-0.073	0.167	-0.139	-0.812	0.675	
VPR	0.602	-0.608	-0.167	0.405	-0.098	0.088	0.096	-0.372	-0.717	0.094	0.180	-0.161	-0.273

696

697 Table 4. Spearman rank correlations (ρ) of parameters in the North Atlantic Deep Water. Values in **bold**: $p < 0.05$. Distance: distance from the stations
 698 closest to the Greenland–Iceland Ridge. Physico-chemical and prokaryotic data are from Teira et al. (2005) and Reinthaler et al. (2006). AOU:
 699 Apparent oxygen utilization; PA: prokaryotic abundance; PHP: prokaryotic heterotrophic production; VA: viral abundance; V1: viral subgroup 1; V2:
 700 viral subgroup 2; V3: viral subgroup 3; VPR: virus-to-prokaryote ratio

	Distance	Temp	Salinity	O ₂	AOU	PO ₄	NO ₃	PA	PHP	VA	%V1	%V2	%V3
Temp	0.556												
Salinity	0.624	0.623											
O ₂	-0.824	-0.730	-0.859										
AOU	0.855	0.624	0.834	0.983									
PO ₄	0.872	0.760	0.814	-0.942	0.029								
NO ₃	0.861	0.792	0.821	-0.938	0.915	0.988							
PA	-0.336	-0.119	-0.700	0.491	-0.517	-0.436	-0.400						
PHP	0.014	-0.134	-0.140	-0.040	0.076	0.041	0.045	-0.182					
VA	-0.809	-0.310	-0.427	0.599	-0.652	-0.655	-0.658	0.303	0.246				
%V1	0.447	0.058	0.150	-0.253	0.308	0.276	0.212	-0.223	0.269	-0.223			
%V2	-0.527	-0.177	-0.245	0.337	-0.382	-0.373	-0.314	0.284	-0.260	0.230	-0.927		

%V3	0.082	0.174	-0.006	-0.002	-0.008	0.119	0.123	0.036	-0.151	-0.051	-0.552	0.275	
VPR	-0.680	-0.147	-0.217	0.385	-0.415	-0.499	-0.506	0.144	0.211	0.875	-0.116	0.141	-0.190

701

702 Table 5. Prokaryotic and viral production, viral infection and virus-mediated mortality of prokaryotic plankton in the North Atlantic Deep Water
703 (NADW). Distance is given in km from the origin of NDAW in the Greenland–Iceland–Norwegian Sea. PHP: heterotrophic prokaryotic production;
704 VP: viral production; **BS: burst size**; FIC: fraction of visibly infected cells; VMMP: virus-mediated mortality of prokaryotes; VP_i: induced viral
705 production; FLC: fraction of lysogenic cells. ND: not determined; NA: not applicable

Station	Distance (km)	PHP ($\times 10^6 \text{ l}^{-1} \text{ d}^{-1}$)	VP ($\times 10^7 \text{ l}^{-1} \text{ d}^{-1}$)	BS	FIC (%)	VMMP _{VP} (%)	VMMP _{FIC} (%)	VP _i ($\times 10^7 \text{ l}^{-1} \text{ d}^{-1}$)	FLC (%)
1	5500	2.95	0.23	24	11.7	3	15.2	0.06	5.8
6	4800	ND	0.21	ND	8.3	ND	10.0	0.59	23.3
9	4000	0.66	0.51	ND	0.6	32	0.6	3.83	4.5
13	2900	1.23	0.98	28	15.6	28	22.2	1.88	29.9
22	1400	0.21	0.80	ND	16.8	139	24.6	0.93	19.5
27	670	1.16	1.49	ND	19.2	46	29.7	3.11	40.1
31	200	0.79	2.40	33	22.0	108	36.6	1.66	15.2
Average	NA	1.17	0.95	28	13.5	59	19.9	1.72	20.5
SD	NA	0.94	0.78	5	7.3	53	12.2	1.36	13.8

706

707 Fig. 1. Study area in the North Atlantic Ocean. Dots: individual stations sampled during the
708 TRANSAT-II

709

710 Fig. 2. Distribution of prokaryotic and viral parameters along the TRANSAT-II cruise in the North
711 Atlantic. Dots: sampling locations; V1, V2 and V3 are viral subgroups 1, 2 and 3, respectively

712

713 Fig. 3. Variation of viral abundance, virus-to-prokaryote ratios (VPR) and 2 viral subgroups (as
714 determined by flow cytometry) in the North Atlantic Deep Water with distance from its formation
715 in the Greenland–Iceland–Norwegian (GIN) Sea. (A) Viral abundance ($p < 0.0001$); (B) VPR ($p <$
716 0.0001); (C) viral subgroup 1 (V1) ($p < 0.005$); (D) viral subgroup 2 (V2) ($p < 0.01$). Regression
717 parameters are given in the plots

718

719 Fig. 4. Variation of viral production, the fraction of infected cells (FIC), induced viral production
720 (VP_i) and fraction of lysogenic cells (FLC) in the North Atlantic Deep Water with distance from its
721 formation in the Greenland–Iceland–Norwegian (GIN) Sea. Data are averages \pm range of duplicate
722 incubations. (A) Viral production ($p = 0.0005$); (B) FIC ($p < 0.05$); (C) VP_i ; (D) FLC. Regression
723 parameters are given in the plots