Mesoscale and microscale spatial variability of bacteria and viruses during a *Phaeocystis globosa* bloom in the Eastern English Channel

J.R. Seymour a,b,*, L. Seuront a, c, M.J. Doubell a, d, J.G. Mitchell a

a School of Biological Sciences, Flinders University, Adelaide, South Australia, 5001 Australia
b Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA 02139, USA
c South Australian Research and Development Institute, Aquatic Sciences, P.O. Box 12, Henley Beach, South Australia, 5024, Australia
d Department of Ocean Sciences, Tokyo University of Marine Science and Technology 4-5-7 Konan, Minato-ku, Tokyo 108-8477, Japan

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**A B S T R A C T**

Sampling was conducted within inshore and offshore sites, characterized by highly dissimilar hydrodynamic and hydrobiological conditions, in the Eastern English Channel. The eutrophic inshore site was dominated by the influence of a dense bloom of the Prymnesiophyceae phytoplankton species *Phaeocystis globosa*, while the offshore site was characterized by more oceanic conditions. Within each site the microscale distributions of chlorophyll *a* and several flow cytometrically-defined subpopulations of heterotrophic bacteria and viruses were measured at a spatial resolution of 5 cm. The inshore site was characterized by comparatively high levels of microscale spatial variability, with concentrations of chlorophyll *a*, heterotrophic bacteria, and viruses varying by 8, 11 and 3.5-fold respectively across distances of several centimeters. Within the offshore site, microscale distributions of chlorophyll *a* and bacteria were markedly less variable than within the inshore site, although viruses exhibited slightly higher levels of heterogeneity. Significant mesoscale variability was also observed when mean microbial parameters were compared between the inshore and offshore sites. However, when the extent of change (max/min and coefficient of variation) was compared between meso- and microscales, the variability observed at the microscale, particularly in the inshore site, was substantially greater. This pattern suggests that microscale processes associated with *Phaeocystis globosa* bloom dynamics can generate heterogeneity amongst microbial communities to a greater degree than large scale oceanographic discontinuities.

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1. Introduction

The Eastern English Channel (EEC) is characterized by two hydrobiologically distinct water masses separated by a tidal frontal boundary (Pingree et al., 1975). The coastal water mass, running parallel to the north-eastern French coastline and named the ‘fleuve côtier’ (i.e. ‘coastal flow’; Brylinski et al., 1996) is influenced by river inputs and strong tidal mixing, and is rich in particulate matter, nutrients, phytoplankton biomass and primary production (Brunet et al., 1992; Dupont et al., 1993). The offshore water mass is generally well stratified and strongly influenced by Atlantic processes (Pingree et al., 1975). Gradients in hydrodynamic and hydrological conditions between the coastal and offshore water masses generate mesoscale variability in the abundance and taxonomic composition of planktonic communities (Pingree et al., 1975; Brunet et al., 1992; Brylinski et al., 1996; Grioche et al., 1999).

The coastal region of the EEC is also characterized by an annual phenomenon that profoundly transforms the physical and biological environment of the *fleuve côtier* (Brunet et al., 1996). Massive blooms of the colonial phytoplankton, *Phaeocystis* sp., occur within the eutrophic coastal waters of France, Belgium, and Holland during April to June (Lancelot, 1995). During *Phaeocystis* blooms copious amounts of exopolymeric mucus, composed primarily of carbohydrates are produced, resulting in the formation of colonial aggregates, up to 2 cm in diameter and often consisting of several thousands of cells (Hamm, 2000; Verity and Medlin, 2003). Subsequently, the coastal water column becomes dominated by thick foamy scums (Jenkinson and Biddanda, 1995; Lancelot, 1995), and as a consequence *Phaeocystis* blooms are widely considered as nuisance events (Chrétiennot-Dinet, 2001).

Due to the large amounts of organic matter released as mucus during blooms, *Phaeocystis* blooms support very active microbial food webs (Rousseau et al., 2000). Bacterial abundance and activity increase during and immediately after *Phaeocystis* blooms

* Corresponding author. Massachusetts Institute of Technology, Department of Civil & Environmental Engineering, 77 Massachusetts Ave, Cambridge, MA 02139, USA.
E-mail address: justins@mit.edu (J.R. Seymour).
The production of mucus exopolymers and the formation of aggregates during *Phaeocystis* blooms are also likely to generate microscale (mm to cm) heterogeneities in the distribution of organic matter. *Phaeocystis* colonies and accumulations of exopolymeric mucus may represent localized hotspots of organic matter for heterotrophic microorganisms. Observations of high levels of bacterial attachment to *Phaeocystis* colonies during the late stages of blooms are in accordance with this prediction (Putt et al., 1994; Becquevort et al., 1998). Diffusion of solutes from colonies into the surrounding water (Ploug et al., 1999) and colony disruption and disaggregation are also expected to provide free-living bacteria with increased concentrations of DOC (Becquevort et al., 1998). Furthermore, the production of large quantities of gelatinous mucus by *Phaeocystis* cells has been shown to fundamentally alter the rheological properties of the surrounding seawater, converting it to a viscous gel-like state, where turbulence-free microenvironments suitable for increased bacterial activity may be created (Jenkinson and Biddanda, 1995). Subsequently, *Phaeocystis* blooms may have significant implications for the small, as well as large-scale dynamics of communities of microorganisms.

2. Materials and methods

2.1. Study sites

Samples were collected from 2 study sites in the Eastern English Channel that differ significantly in hydrodynamic conditions and extent of influence from the annual *Phaeocystis globosa* bloom. The inshore station (50° 40′ 75 N, 1° 31′ 17 E) is situated approximately 1.8 km from the north-eastern coast of France and is characterized by high levels of tidal mixing, eutrophic conditions, and is strongly influenced by *Phaeocystis* blooms. The offshore site (50° 40′ 75 N, 1° 24′ 60 E) is situated 9.3 km from the coast and is characterized by more oceanic conditions and lower concentrations of nutrients and chlorophyll. Inshore and offshore stations were sampled on April 21 and 22, respectively. At each study site bulk physical conditions (temperature and salinity) were measured from the surface to the bottom with a Sea-Bird SBE 25 Sea logger CTD probe.

2.2. Microscale sampling device

To measure the microscale distributions of chlorophyll *a* and microorganisms in each of the sampling sites, a purpose-designed sampling device was applied. The design of the device was based on sampling systems previously employed to measure the microscale spatial distributions of bacteria and phytoplankton (Seymour et al., 2000, 2004; Waters et al., 2003) and consisted of a 10 × 10 array of 50 ml syringes, separated at a spatial resolution of 5 cm. The pneumatically operated device was attached to a series of electric pumps allowing for the simultaneous collection of 100 samples across an area of 0.2 m². Samples were taken from a depth of 1 m at each of the sampling sites.

2.3. Sample analysis

Concentrations of dissolved inorganic nitrogen (NO₂⁻, NO₃⁻), silicate (SiO₄⁻) and phosphate (PO₄³⁻) in 10 ml samples were determined using an Alliance Integral Auto-Analyzer. Subsamples (50 ml) collected using the microscale sampling device were divided to allow for analysis of chlorophyll *a* and bacterial and viral abundance. For chlorophyll *a* analysis, 25 ml subsamples of seawater were filtered onto glass fiber filters (Whattman GF/C, 0.45 μm). Filters were immediately transferred to plastic tubes containing 5 ml of 100% N,N-dimethyformamide (DMF), and chlorophyll concentrations were determined using a Turner 450 fluorometer.

For enumeration of bacterio-plankton and virio-plankton within samples, 1 ml aliquots were fixed with paraformaldehyde (2% final concentration) for 20 min, quick frozen in liquid nitrogen, and stored at −80 °C. Populations of bacteria and viruses were identified and enumerated using flow cytometry. Prior to flow cytometry, samples for bacterial analysis were stained with SYBR-I Green solution (1:10,000 dilution; Molecular Probes, Eugene, OR), and incubated in the dark for 15 min (Marie et al., 1997, 1999a,b). Samples for virus analysis were diluted (1:50) in 0.02 μm filtered TE buffer (10 mM Tris, 1 mM EDTA, pH 7.5), stained with SYBR-I Green (5:100,000) and incubated in the dark for 15 min (Marie et al., 1999a). Fluorescent beads of 1 μm diameter (Molecular Probes, Eugene, OR), were added to all samples in a final concentration of approximately 10⁵ beads ml⁻¹ (Gasol and del Giorgio, 2000), and all measured cytometry parameters were normalized to bead concentration and fluorescence.

All flow cytometry was conducted using an Epics Elite flow Cytometer (Beckman Coulter Inc., Fullerton, CA, USA) at the Institut de Recherche sur le Cancer de Lille (IFR114 IMPRT). For each sample, forward scatter (FSC), side scatter (SSC), green (SYBR-I) fluorescence, red fluorescence, and orange fluorescence were acquired, and machine set-up followed the protocols described by Marie et al. (1999b). Sample acquisition was run until at least 50 μl of sample was analyzed at an event rate of <800 s⁻¹. Individual viral and bacterial populations were separated according to variations in SYBR-Green fluorescence (indicative of nucleic acid content) and SSC (Marie et al., 1997, 1999a,b). Data for individual subsamples was collected in list-mode files, and populations were identified and enumerated using Win Midi 2.8 (© Joseph Trotter) flow cytometry analysis software.
2.4. Statistical analysis

As the spatial distributions of the microbial community were significantly non-normal (Kolmogorov–Smirnov test, P < 0.05) in most instances, non-parametric statistics were employed throughout this work. Comparisons between sites were carried out using the Wilcoxon–Mann–Whitney U-test (WMW test) (Zar, 1984), and correlations between different microbial variables within microscale profiles were investigated using Kendall’s coefficient of rank correlation, τ (Kendall and Stuart, 1966).

To obtain a simple quantification of the degree of microscale variability observed for a given population within microscale profiles we calculated the relative change in abundance of the population (max/min) and a coefficient of variation (CV) for that change. The Kolmogorov–Smirnov test for normality, and related skew and kurtosis values were also calculated to investigate the nature of the distributions of each population. All statistical analyses were performed using SPSS Version 11.0 statistical software.

3. Results

3.1. Mesoscale variability: comparison of study sites

The two sampling sites were characterized by markedly different environmental conditions and microbial communities (Table 1). No vertical stratification was observed in the distribution of temperature and salinity at either inshore and offshore stations. This is congruent with the strong turbulent conditions and the well-mixed water column previously observed at the same stations (Seuront et al., 1999, 2002). The mean temperature and salinity levels for the offshore and inshore sites were 8.1 °C and 35.2 PSU, and 9.6 °C and 34.0 PSU respectively. Concentrations of NO3, NO2, PO4, and SiO4 all differed significantly (p < 0.01) between the inshore and offshore sites.

At the time of sampling, the phytoplankton community at the inshore site was dominated by Phaeocystis globosa, which made up 40 –50% of the total phytoplankton community (Seuront et al., 2006). In the inshore site, P. globosa colonies occurred in concentrations of 1200 colonies l−1, compared to only 500 l−1 in the offshore site. The characteristics of the P. globosa colonies also varied between sites, with the inshore site dominated by large colonies, reaching 750 µm in diameter, and the offshore site dominated by significantly smaller colonies (50–80 µm).

Mean concentrations of chlorophyll a, bacteria and viruses were all significantly (p < 0.01) higher at the inshore site than the offshore site, reaching concentrations of 46.6 µg l−1, 3.3 × 109 ml−1 and 5.1 × 107 ml−1 respectively (Table 1). The population characteristics of the bacterial and viral communities, determined using flow cytometry, also differed between the two sites (Fig. 1). Relative abundances of bacterial and viral subpopulations in each of the study sites are presented in Table 2. At each site, 4 discrete subpopulations of bacteria could be differentiated in all samples according to differences in SYBR Green fluorescence, corresponding to variability in nucleic acid content (Fig. 1a,b). The B1 and B2 populations were characterized by lower levels of green fluorescence, and we suggest that these groups represent subpopulations comprising the Low-DNA (LDNA) bacterial subgroup identified in most aquatic water samples (Li et al., 1995; Jellett et al., 1996; Gasol et al., 1999). The B3 and B4 populations exhibited higher levels of green fluorescence and are alternatively predicted to represent members of the High-DNA (HDNA) bacterial subgroup (Gasol et al., 1999). The bacterial community inhabiting the inshore site was dominated by this HDNA group, which reached 3 × 109 ml−1 and 92% of the total bacterial population. Alternatively, within the offshore site only 63%, corresponding to 0.95 × 109 ml−1, of bacteria were HDNA. According to Wilcoxon–Mann–Whitney U-tests the proportion of HDNA bacteria, and the concentrations of all subpopulations of heterotrophic bacteria, with the exception of the B1 group, differed significantly (p < 0.01) between the inshore and offshore sites.

The virus community was also divided into two subpopulations, according to different peaks apparent on histogram plots of SYBR Green fluorescence, which correspond to discrete populations with differing nucleic acid content (Fig. 1c,d) (Marie et al., 1999a). Viral subpopulations corresponding to low DNA (V1) and high DNA (V2) groups (Larsen et al., 1994) were present in all samples from both study sites. Within the inshore samples, the viral community was dominated by the V2 group, which occurred in concentrations of 3.8 × 109 ml−1 and comprised 73% of the total viral community (Fig. 1d). Alternatively, within the offshore samples the V1 and V2 populations occurred in similar concentrations, with the V2 population representing approximately 50% of the total viral community (Fig. 1c). Total viral abundance, as well as the numbers of V1 and V2 viruses, and the proportion of V2 viruses differed significantly (p < 0.01) between the inshore and offshore sites. The virus:bacteria ratio (VBR), calculated from total viral and bacterial abundances, also varied significantly (p < 0.01) between study sites, with higher VBR (19.3) observed in the offshore samples (Table 1).

3.2. Microscale variability

Relative changes in abundance, coefficients of variation, skew, and kurtosis values for each of the populations are presented in Table 2. At the inshore site, microscale spatial patterns for all microbial populations were characterized by the presence of single and multiple point hotspots in abundance, where concentrations were sometimes more than 4 times higher than background levels (Fig. 2). Chlorophyll a concentration varied by 8-fold and exhibited gradients in abundance extending over several centimeters (Fig. 2a). The total concentration of heterotrophic bacteria varied by over 11-fold and each of the bacterial subpopulations exhibited high levels of microscale spatial variability (Fig. 2c−f). Although often exhibiting dissimilar features (e.g. locations of hotspots) in microscale distributions (Fig. 2), all bacterial subpopulations, with the exception of the B1 and B3 groups, were weakly, but significantly, correlated to one another (mean τ = 0.260, p < 0.05). All of the bacterial subpopulations were non-normally distributed (p < 0.05) and exhibited significant skew and kurtosis values, indicative of ‘peaky’ distributions (Table 2). None of the bacterial subpopulations, including total bacterial abundance, were significantly correlated (p > 0.05) to the distribution of chlorophyll a. The proportion of HDNA bacteria (B3 and B4) ranged between 78.5 and 97% within the microscale profile and was not significantly correlated to any other parameters.

### Table 1

<table>
<thead>
<tr>
<th>Site</th>
<th>Chl a (µg l−1)</th>
<th>Bacteria (×109 ml−1)</th>
<th>% HDNA</th>
<th>Viruses (×107 ml−1)</th>
<th>% V2</th>
<th>VBR</th>
<th>NO3 (µM)</th>
<th>NO2 (µM)</th>
<th>SiO4 (µM)</th>
<th>PO4 (µM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Offshore</td>
<td>8.1 ± 2.7 SD</td>
<td>1.5 ± 0.13 SD</td>
<td>63.0 ± 2.7 SD</td>
<td>2.9 ± 0.9 SD</td>
<td>50.1 ± 6.2 SD</td>
<td>19.3 ± 6.7 SD</td>
<td>0.06 ± 0.008 SD</td>
<td>4.1 ± 0.7 SD</td>
<td>2.8 ± 0.9 SD</td>
<td>0.19 ± 0.08 SD</td>
</tr>
<tr>
<td>Inshore</td>
<td>46.6 ± 10.5 SD</td>
<td>3.3 ± 0.51 SD</td>
<td>91.9 ± 2.6 SD</td>
<td>5.1 ± 11.1 SD</td>
<td>73.2 ± 5.8 SD</td>
<td>16.7 ± 12.1 SD</td>
<td>2.2 ± 1.1 SD</td>
<td>0.23 ± 0.4 SD</td>
<td>1.9 ± 0.87 SD</td>
<td>0.4 ± 0.04 SD</td>
</tr>
</tbody>
</table>
The distributions of viruses were also characterized by high levels of microscale spatial heterogeneity, with distributions dominated by strong abundance hotspots (Fig. 2b) and significant skew and kurtosis values (Table 2). The viral subpopulations exhibited significantly different spatial distributions to one another \( (p > 0.05) \), and neither of the virus populations were significantly correlated \( (p > 0.05) \) to any of the bacteria populations or chlorophyll \( \alpha \).

At the offshore site, levels of variability amongst the microbial populations were generally not as strong as within the inshore site. Chlorophyll \( \alpha \) levels were 5.75 times lower in the offshore site than the inshore site, and the change in concentration within the microscale profile was also slightly lower (Table 2). The bacterial population was much less heterogeneous in the offshore site, only varying by 1.8-fold across the profile, and each of the subpopulations exhibited much lower CV and max/min values than were observed in the inshore site (Table 2). Unlike the inshore samples, all bacterial subpopulations, with the exception of the B4 group, were normally distributed (Table 2). Weak, but significant, correlations \( (\text{mean } r = 0.246, p < 0.05) \) were observed between all of the bacterial subpopulations, with the exception of the B2 and B4 groups. The proportion of HDNA (B3 and B4) bacteria ranged between 51 and 71% and was not correlated to any other parameters. None of the bacterial subpopulations were significantly correlated \( (p > 0.05) \) to the distribution of chlorophyll \( \alpha \). Unlike the bacterial populations, the viruses exhibited significant skew and kurtosis values and slightly higher levels of microscale heterogeneity in the offshore site (Table 2).

Similar to the inshore site, the viral subpopulations were not correlated \( (p > 0.05) \) to any another, or to the distributions of any of the bacterial populations or chlorophyll \( \alpha \).

### 3.3. Comparison of variability between scales

In most cases the microscale variability in the abundance and composition of the microbial communities within each of the
sampling sites was more intense than the mesoscale variability observed between the two sites (Fig. 3). Where relative changes in abundance (max/min) of parameters were compared, the highest levels of variation amongst bacterial subpopulations and chlorophyll $a$ concentration were observed within the inshore site. Alternatively, the viral populations were most variable within the offshore site. Mesoscale changes in abundance of the total bacterial community and the B2 and B3 subpopulations were greater between the two sites than the microscale variability observed within the offshore site. The mesoscale variability never exceeded the microscale variability observed within the inshore site for any of the individual populations. However, the shift in the mean relative proportion of HDNA (B3 and B4) bacteria between sites (29%) was higher than was observed within the inshore (18.5%) and offshore sites (20%).

4. Discussion

4.1. Mesoscale variability

We observed significant shifts in the concentrations of nutrients and chlorophyll $a$, and the abundance, activity and constitution of
bacterial and viral communities over a distance of 7.5 km in the Eastern English Channel (Table 1). These changes are congruent to patterns previously observed for phytoplankton and zooplankton populations within this region (Brunet et al., 1996; Brylinski et al., 1996; Grioche et al., 1999) and are likely to have occurred in response to either the dissimilar hydrobiological conditions in the two habitats (Pingree et al., 1975; Brylinski et al., 1996), or the dissimilar characteristics of the Phaeocystis globosa community at each site.

Chlorophyll a levels were over 5 times higher at the inshore site than the offshore site, due primarily to the Phaeocystis globosa bloom that dominated the coastal environment during the sampling period (Seuront et al., 2006). Inorganic nutrient concentrations are also predicted to be higher within the fleuve côtier, which is generally characterized by eutrophic conditions due to riverine inputs of nutrients and suspended matter (Brunet et al., 1996). However, during this study only NO2 and PO4 concentrations were elevated within the inshore region, while NO3 and SiO4 levels were actually higher in the offshore site. It is likely that the low concentrations of SiO4 and NO3 observed in the inshore site occurred following depletion of these nutrients during the spring diatom and Phaeocystis blooms that dominate the inshore site.

The relative proportions of the bacterial and viral populations varied by up to 8-fold across distances of a few centimeters, and microscale distributions were characterized by the presence of concentration gradients, as well as hotspots and coldspots (Fig. 2).

4.2. Microscale variability

The levels of microscale spatial variability observed here are typically higher than we have previously observed in other habitats (Seymour et al., 2000, 2004, 2005, 2007). Chlorophyll a levels varied by up to 8-fold across distances of a few centimeters, and microscale distributions were characterized by the presence of concentration gradients, as well as hotspots and coldspots (Fig. 2).

Centimeter-scale distributions of chlorophyll have been measured...
Previously (Waters and Mitchell, 2002; Waters et al., 2003), but to our knowledge have not been investigated within the context of a Phaeocystis bloom. We found that the degree of variability, and the nature of the microscale distribution patterns (skew, kurtosis etc.), were comparable between the inshore and offshore sites (Table 2), suggesting that the dynamics of the Phaeocystis globosa bloom did not generate greater levels of microscale variability in chlorophyll a.

Unlike chlorophyll, the microscale spatial distributions of the bacterial community were markedly dissimilar between the inshore and offshore sites (Fig. 2). Within the inshore site bacterial abundance varied by over 11-fold, compared to a less than 2-fold change in abundance in the offshore site. As we have observed previously (Seymour et al., 2004, 2005, 2007), the spatial distributions of the bacterial subpopulations were more variable than the total bacterial abundance, confirming that bacterial heterogeneities can be underestimated by traditional counting methods (e.g. DAPI counts etc.), because discrete functional groups are likely to display more dynamic characteristics than the total average counts (Seymour et al., 2004). The populations inhabiting the inshore site were also almost always more variable than the offshore populations.

The dominant feature of the microscale distributions of bacteria within the inshore site was intense abundance hotspots (Fig. 2). The most immediate explanation for these hotspots is bacterial attachment to the abundant and large Phaeocystis colonies at this site, in response to the elevated concentrations of organic matter within the colonial matrix. The biomass and activity of bacterial communities attached to colonies are often substantially higher than in the free-living phase during Phaeocystis blooms (Putt et al., 1994; Becquevort et al., 1998). However, it is notable that the most intense hotspots of bacteria observed here did not correspond to hotspots in chlorophyll a, and no significant correlations between chlorophyll a and any of the bacterial subpopulations were observed. Davidson and Marchant (1987) observed strong negative correlations between bacterial abundance and chlorophyll a during a Phaeocystis bloom, which they attributed to the bactericidal properties that have sometimes been ascribed to Phaeocystis colonies. During bloom conditions, Phaeocystis cells synthesize significant amounts of acidic acid, which in large quantities is toxic to marine bacteria (Sieburth, 1959, 1960) and may prohibit bacterial attachment to colonies (Davidson and Marchant, 1987; Verity et al., 1988).

However a number of other studies have demonstrated that the influence of Phaeocystis derived acidic acid on associated bacterial communities is negligible (Putt et al., 1994; Osinga et al., 1997; Noordkamp et al., 2000). Another potential explanation for the lack of coherence between chlorophyll a concentrations and the bacterial hotspots observed here is that Phaeocystis cells generally only occupy a small volume (≤10%) of the gelatinous matrix within colonies, and disintegration of colonies will potentially supply the water column with large quantities of cell-free mucus aggregates (Lancelot, 1995). Furthermore, the nutritional value and biodegradability of Phaeocystis derived organic material can vary considerably (Thingstad and Billen, 1994; Janse et al., 1996; Osinga et al., 1997), and it has been shown that the extent of bacterial attachment to fragmented aggregates during the late stages of blooms is often greater than attachment to healthy colonies (Lancelot, 1995). Therefore, bacterial colonization of these sticky aggregates (Thingstad and Billen, 1994), as well as association with patches of DOC produced during colony disintegration (Billen and Fontigny, 1987), may be responsible for the formation of the hotspots observed here. Alternatively, top-down influences, such as increased grazing pressure on bacteria by some micro zooplankton, as a consequence of Phaeocystis colony formation, could also have contributed to the high levels of spatial heterogeneity in the inshore site.

Like the bacterial populations, distributions of viruses were characterized by microscale heterogeneity. However, discrete abundance hotspots were apparent in both the inshore and offshore sites, and unlike the case for bacteria, the Phaeocystis bloom in the inshore site apparently did not facilitate higher levels of microscale patchiness of viruses. The microscale distributions of the V1 and V2 populations were not correlated in either site, suggesting that they represent ecologically discrete populations.

Due to the apparent lack of microscale association between the virus and potential host populations, it is difficult to derive possible mechanisms for the generation of the hotspots of viruses observed here. Virus hotspots may represent recent localized zones of enhanced viral lysis (Seymour et al., 2006), or alternatively, as observed by Jacobsen et al. (1996), elevated concentrations of viruses may become entrapped in the mucilage material derived from Phaeocystis colonies.

Although the microscale data sets compared here were obtained from a single deployment of the microscale sampling device in each system, the strong disparities in community characteristics and spatial statistics point towards a clear effect of the Phaeocystis bloom on the microbial community during the time of sampling. The degree and extent of these shifts are likely to hinge upon a range of biotic and abiotic variables, which are likely to shift with physical conditions and phytoplankton community succession in this region of the EEC.

4.3. Comparison of scales and ecological implications

Both the mesoscale and microscale patterns observed here are likely to have significant ecological implications at a number of levels. Mesoscale variability in chlorophyll concentrations and bacterial abundance and activity will influence bulk rates of primary and secondary production, which will ultimately affect carbon fluxes and food web structure in the Eastern English Channel (Thingstad and Billen, 1994). Large scale shifts in the abundance and composition of viral communities, like those observed here, have previously been implicated in the decline of phytoplankton blooms in the English Channel (Wilson et al., 2002).

At the microscale, hotspots of bacterial abundance and activity may be representative of microhabitats characterized by increased remineralization of Phaeocystis derived organic matter. The intensity and frequency of these hotspots will ultimately determine the proportion of carbon that is exported to the sediments or retained in the pelagic food web. The establishment of bacterial micro zones on Phaeocystis aggregates will also create microscale gradients in oxygen and nutrients (Ploug et al., 1999) which may significantly alter nutrient cycling process within the surrounding water column (Paerl and Pinkney, 1996). Phaeocystis aggregates represent microcosms accommodating well developed microbial food webs (Thingstad and Billen, 1994), and microscale patchiness of organisms attached to aggregates and in the surrounding water column will fundamentally alter predator–prey and virus–host dynamics (Rothschild, 1992), and may subsequently modify the flow of matter through the microbial loop (Azam et al., 1983).

The patterns observed here are in accordance with the results of previous temporal experiments (Seymour et al., 2005), and indicate that the extent of microscale patchiness amongst marine microbial communities can sometimes be comparable to, or greater than, the variability observed at larger scales. These findings are particularly pertinent within this specific case because significant mesoscale variability was predicted due to the fundamentally dissimilar oceanographic features of the two water masses compared. The microscale patchiness observed here, particularly within the inshore site, implies that events such as Phaeocystis blooms can sometimes induce higher levels of spatial heterogeneity amongst
marine microbial communities than is caused by large scale physical discontinuities.

References


