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Extreme spatial variability in marine picoplankton and its consequences for interpreting Eulerian time-series

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A high-resolution mesoscale spatial survey of picoplankton in the Celtic Sea, using flow cytometry, reveals cell concentrations of *Synechococcus* spp. cyanobacteria and heterotrophic bacteria that vary up to 50-fold over distances as short as 12 km. Furthermore, the range of abundances is comparable to that typically found on seasonal scales at a single location. Advection of such spatial variability through a time-series site would therefore constitute a major source of 'error'. Consequently, attempts to model and to investigate the ecology of these globally important organisms *in situ* must take into account and quantify the hitherto ignored local spatial variability as a matter of necessity.

Keywords: bacterioplankton; cyanobacteria; flow cytometry; patchiness

1. INTRODUCTION

Despite their minute size (less than 2 μm in length), picoplankton can be dominant organisms in marine ecosystems. Their cells outnumber all but viruses, and they contribute up to 60% of the global marine primary production (Platt *et al.* 1983; Li 1994). They are, therefore, key components of the marine ecosystem, with a major role in the global carbon cycle. Certain species have been isolated and studied (Waterbury *et al.* 1979; Chisholm *et al.* 1988; Partensky *et al.* 1999), but little is currently known about the characteristic temporal and spatial scales of these organisms *in situ*. Time-series are a vital tool for focusing on the dominant processes and interactions in the ecosystem at specific times and locations. By monitoring the fluctuating abundance of picoplankton, characteristic phenomena such as synchronized division (Vaulot & Marie 1999) and seasonal succession can be identified and studied (Jacquet *et al.* 1998; Li 1998; Grégori *et al.* 2001; Li & Dickie 2001). This, though, requires each datum to accurately represent the local abundance of picoplankton at that time.

The degree of spatial variability around a time-series station is rarely investigated. Thus, the unverified assumption is made that the local heterogeneity is less than the daily or seasonal variability, despite large amounts of observational and empirical evidence for the ubiquity of spatial variability (for reviews see, for example, Denman & Dower 2001; Martin 2003). We demonstrate here that this fundamental assumption may not be true: the abundance of both autotrophic and heterotrophic picoplankton can fluctuate spatially, over distances as small as 12 km, with extremes equivalent to those found on seasonal scales.

2. MATERIAL AND METHODS

Over 10–17 July 2004 a high-resolution mesoscale spatial survey of near-surface picoplankton distributions was carried out in the Celtic Sea. An area of approximately 120 km in diameter (figure 1*a*) was sampled repeatedly, using triangular paths, whenever the weather allowed, each with an apex at 50°45.54′ N, 7°1.527′ W. Observations along a typical transect are shown in figure 1*b–f*. Water was continuously pumped from a depth of 3 m (a SeaBird SBE38 temperature probe recorded temperature at the mouth of the pump), which was within the mixed layer throughout the cruise, thereby avoiding 'contamination' by vertical heterogeneity. Samples were taken from this stream and fixed every 12 min. Picoplankton were then enumerated using a flow cytometer. The methods used were slight modifications of those in Olson *et al.* (1993) and Marie *et al.* (1997). Further details are available from the authors on request. Although care needs to be exercised in giving definite names to measured organisms in the absence of a full suite of identification tests, based on the most likely situation *Synechococcus* spp. and non-autofluorescent bacteria are hereafter referred to as *Synechococcus* and heterotrophic bacteria, respectively, for convenience.

The seasonal time-series also reported here was carried out at the L4 Eulerian station (http://www.pml.ac.uk/L4) in the English Channel (50°15′ N, 4°15′ W, 6 km off Plymouth, UK) from August 1998 to December 2001, with a shortest time between samples of 4 days, but generally with samples taken one week apart. Water samples were collected from 2 m depth (total water depth 55 m) and picoplankton abundance was determined using flow cytometric techniques similar to those described above for the spatial survey.

3. RESULTS

The abundances of *Synechococcus* and heterotrophic bacteria in the Celtic Sea throughout the cruise are shown in figure 2*a*,*b*, respectively. The large amount of variability is striking. The *Synechococcus* population fluctuates more than 60-fold, with cell concentrations varying between 2500 and 150 000 cells ml^{-1} over the 7-day sampling period. At times, the concentrations change incredibly abruptly: near the start of day 193 (11 July) the population changes from 5000 cells ml^{-1} to in excess of 90 000 cells ml^{-1} in just 96 min. As the ship's speed was 2 m s^{-1} this signifies a greater than 50-fold change in abundance in just under 12 km. Often, dramatic increases in abundance are reversed over a similar length-scale, giving rise to extreme spikes in abundance; two examples occurred on the morning of day 196 (14 July). The high resolution of these data gives confidence that such spikes are genuine features of the plankton's distribution, since each spike typically comprises 10 or more data points. The variability in the heterotrophic bacterial abundance is also dramatic. The population varies between 150 000 and 4 400 000 cells ml^{-1} over the cruise—a 30-fold variation. Although extreme variations are less frequent (but as a consequence more marked) than in the *Synechococcus* data, the 'background' variation for heterotrophic bacteria still lies between 350 000 and 1 000 000 cells ml^{-1}, a threefold fluctuation. It should also be noted that heterotrophic bacteria

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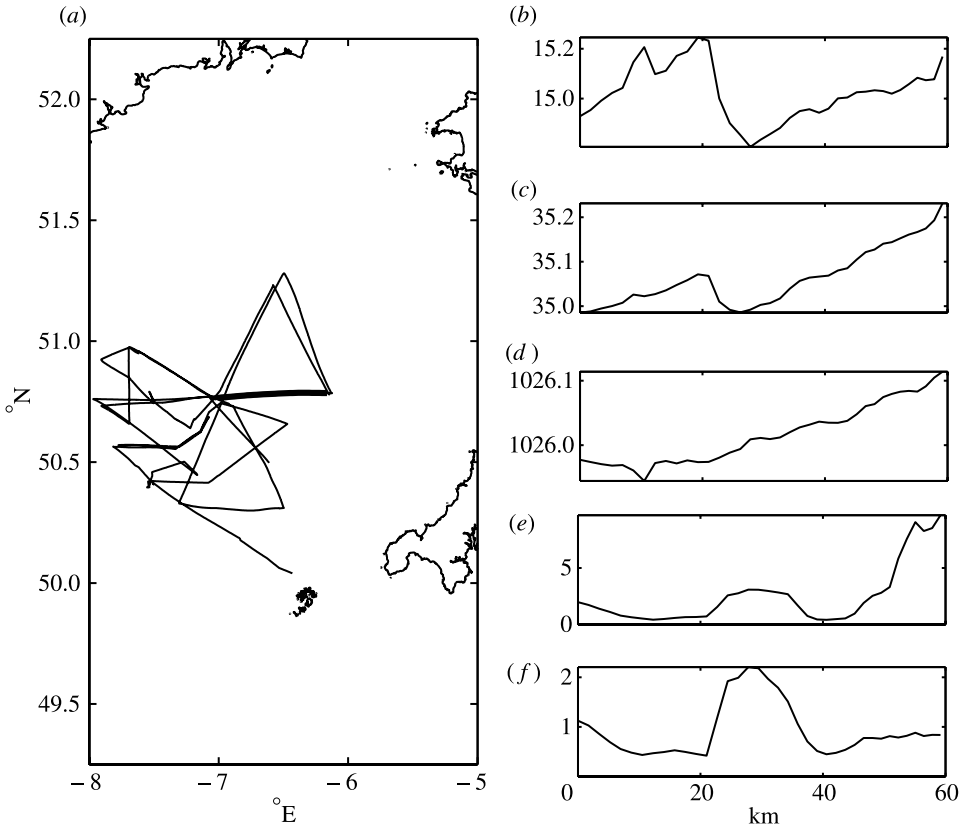

Figure 1. (*a*) Region and track of survey. The western edges of England and Wales and southern edge of Ireland are visible. (*b*) Temperature (°C), (*c*) salinity (psu), (*d*) density (kg m^{-3}), (*e*) *Synechococcus* ($\times 10^4$ cells ml^{-1}) and (*f*) heterotrophic bacteria ($\times 10^6$ cells ml^{-1}) along a typical transect (marked in bold on (*a*)).

include a more phylogenetically diverse group of organisms than *Synechococcus*, which may disguise variability. Correlations with density, salinity and temperature 'explained' at most 44% (*Synechococcus* and temperature) of the cell number variability and as little as 1% (heterotrophic bacteria and density). There was no apparent diel or tidal signal in the data. The only general trend was the suggestion of lower concentrations of *Synechococcus* in the centre of the survey throughout the cruise.

Fitting an exponential relationship to the abundance versus time profile for the abrupt changes in the *Synechococcus* distributions (such as at the start of day 193) yields a mean for all such increases of 24 ± 15 d^{-1}. Typical growth rates for *Synechococcus* are 1.0 d^{-1} (e.g. Jacquet *et al.* 1998). These sharp gradients must, therefore, be spatial in origin and cannot be due to rapid local population increase. Further evidence for this can be found in the spiky nature of the distribution, already discussed, which would require an equally dramatic cause of population decline in the organism's population. Neither is such variation due to mixing of deeper water that might contain a higher concentration of cells: both night and day vertical CTD (conductivity, temperature and depth) casts (not shown) revealed a mixed layer depth that was remarkably stable at 30 m throughout the cruise. Strong correlations between repeated survey legs (not shown) also testify to the spatial nature of the variability.

Figure 2*c*,*d* shows the composite seasonal variation in *Synechococcus* and heterotrophic bacteria abundances at the L4 station. *Synechococcus* numbers fluctuate from below the limit of detection (50 cells ml^{-1}) to 47 000 cells ml^{-1}. Heterotrophic bacterial numbers vary between 170 000 and 1 600 000 cells ml^{-1}. Even taking into account the seasonal signal apparent in heterotrophic bacteria, the data are still very noisy with many large spikes. It is by no means intended that direct comparisons be drawn between the Celtic Sea data and the L4 time-series—the L4 site differs in having much shallower water and much stronger tidal mixing that may actually damp variability. Rather, the L4 data are presented to illustrate the typically noisy nature of weekly (or more sporadically) sampled time-series. The visual similarity to the Celtic Sea data, however, where the variability is known to be spatial in origin, raises the question of whether the very significant time-series 'noise' is due to spatial variability advected through the site.

4. DISCUSSION

The data presented here reveal that abundances of the cyanobacteria *Synechococcus* and of heterotrophic bacteria vary on spatial scales as small as 12 km, over a range equivalent to the seasonal extent of the fluctuations seen in fixed point time-series data.

But is the observed variability of picoplankton in the Celtic Sea exceptional? Are spatial fluctuations typically lower in other locations? It is difficult to address these questions as very few high-resolution mesoscale surveys of picoplankton have been carried out. Sparsely sampling an area roughly 500×200 km

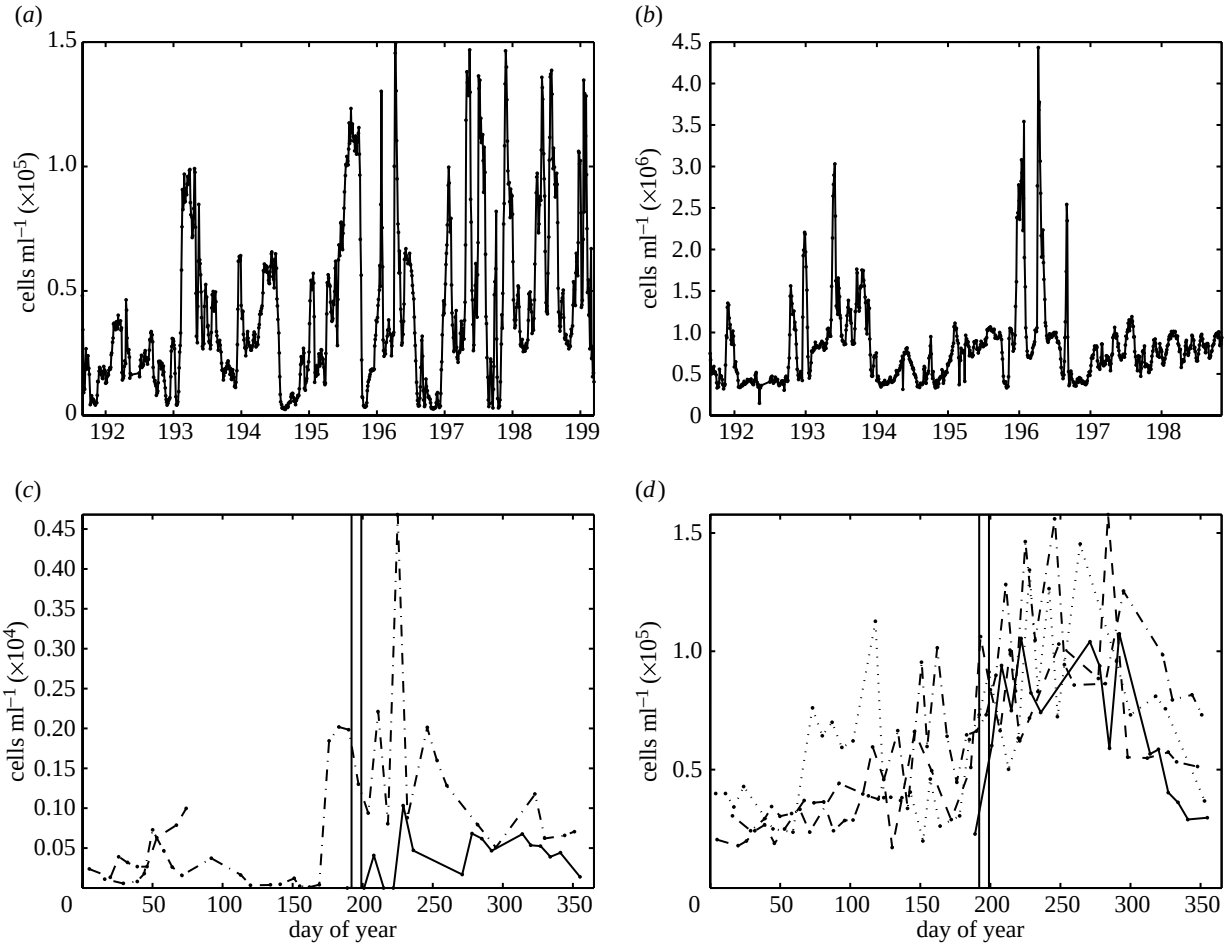

Figure 2. Cell abundances (cells ml^{-1}) for (*a*) *Synechococcus* and (*b*) heterotrophic bacteria in the Celtic Sea between UK and Ireland in July 2004. Day 192 is equivalent to 10 July. Also shown are cell abundances (cells ml^{-1}) for (*c*) *Synechococcus* and (*d*) heterotrophic bacteria for Station L4 in the English Channel. Parts (*c*) and (*d*) show the seasonal variation of cell abundance using data for the years 1998 (solid), 1999 (dashed), 2000 (dotted) and 2001 (dash-dotted). No data are available for 2000 for *Synechococcus*. The tall narrow boxes shown in (*c*) and (*d*) indicate the Celtic Sea sampling period for comparison.

in the North Sea revealed bacterial abundance varying between 94 000 and 3 100 000 cells ml^{-1} (Zubkov *et al.* 2002). No gradients as sharp as those witnessed here were found at 20 km, the smallest scale of sampling. Only 134 samples were obtained for that survey, however, compared with the 890 obtained at 14 times the spatial resolution in the Celtic Sea survey. On an hourly sampling, 2500 km transect through the Mozambique Channel *Synechococcus* cell abundances were found to vary from 4500 to 57 000 cells ml^{-1} (Zubkov & Quartly 2003). On small scales, however, the greatest change was from 23 000 to 42 000 cells ml^{-1} over a distance of 19 km. As the Mozambique survey was a linear transect, it is impossible to determine whether the full variability witnessed along the transect would have been repeated at the smallest scales if a more detailed local survey had taken place, or if it was just a result of large-scale environmental gradients. Similar to the Celtic Sea study, however, no significant correlation was found between cell abundance and the physical properties of the water.

Station L4 was chosen for comparison here purely because it offers the time-series closest geographically to the Celtic Sea. As previously stressed, it should not be compared directly. It is just for illustration. Other time-series display similar seasonal variability. Data from the Bedford Basin, Canada (Li 1998; Li & Dickie 2001), Bay of Marseilles (Grégori *et al.* 2001) and the western subarctic North Pacific (Liu *et al.* 2002) show *Synechococcus* abundance ranging annually from undetectable to 70 000–450 000 cells ml^{-1}, while heterotrophic bacteria vary in abundance between 140 000 and 1 300 000 cells ml^{-1}. The level of noise in these time-series varies, however. For example, the Bay of Marseilles data are very spiky, while that in the Bedford Basin has a strong seasonal cycle with occasional large spikes. Care is needed not to make too strong a comparison, though, given the coarse sampling period, as is apparent comparing figure 2*a* with figure 2*c* for example. Also, it should not be forgotten that spatial variability may vary both seasonally and with geographical location. Currently, we simply do not know and therefore cannot quantify its impact over annual scales.

Attributing definite causes to the patchiness reported here is currently impossible. A shifting balance between nutrient-controlled growth and losses due to senescence, protozoan predation and viral infections is most likely, but we do not have rates or viral abundance data to quantify the relative influences.

We argue that spatial variability must be regarded as a potentially serious source of error in time-series data. Take, for example, the *Synechococcus* cell abundance data from the Celtic Sea. It has been shown that sites just 12 km apart can have concentrations as different as 5000 and 90 000 cells ml^{-1}. Hypothetically, a mean current of only 2 cm s^{-1} would be required to cause these two concentrations to be logged as consecutive data in a weekly sampling time-series station in a region with such variability. Furthermore, averaging over a 'suitable' period will not remove the 'noise' coming from spatial variability. The data from the Celtic Sea are significantly non-Gaussian (not shown), so simple averaging methods would give a poor estimate of the true mean. Only a spatial survey could provide the information needed to carry out an accurate 'smoothing' of the time-series data.

Should further surveys show that the degree of variability in picoplankton populations reported here at small scales is typical, great care will have to be exercised in interpreting time-series data. A recommendation arising from this work is that samples at such fixed stations should be augmented with a high-resolution mesoscale spatial survey of the area, preferably several times during different seasons. Only in this way can the errors introduced into the dataset by advection of spatial variability be quantified and taken into account. Failure to do so will jeopardize attempts to understand the dynamics of the ecosystem and will undermine attempts to model this key component of the marine carbon cycle.

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