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Phytoplankton patch patterns: Seascape anatomy in a turbulent ocean

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Abstract

Marine phytoplankton experience competition, predation, infection and aggregation occurring across distances of micrometres to centimetres. However, the consequences of these interactions influence global processes, such as climate and fisheries productivity. There is a long-standing default assumption that these global processes cannot be traced to plankton distributions and interactions below a few metres because of the homogenising effect of turbulence [Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–146.; Siegel, D.A., 1998. Resource competition in a discrete environment: Why are plankton distributions paradoxical? Limnol. Oceanogr. 43, 1133–1146.]. We show that, in active turbulence, phytoplankton patches, on the order of 10 cm, have repeatable asymmetry and regular spacing over distances of centimetres to tens of metres. The regularity and hierarchical nature of the patches in mixed ocean water means that phytoplankton are distributed in a dynamic, but definite seascape topography, where groups of patches coalesce between intermittent turbulent eddies. These patches may link large scale processes and microscale interactions, acting as fundamental components of marine ecosystems that influence grazing efficiency, taxonomic diversity, and the initiation of aggregation and subsequent carbon flux.

1. Introduction

Phytoplankton distributions provide fundamental information about and insight into physical and biological processes in aquatic ecosystems (Denman et al., 1977; Steele, 1989; Abraham et al., 2000). At the global scale, they define rich ocean regions and outline ocean biomes (Falkowski et al., 1998). At mesoscales, they highlight the importance of upwelling for primary productivity, the role of mixing in dispersion and the ability of fronts to confine and accumulate phytoplankton (Yoder et al., 1994). Below a few metres, often called the microscale, there is a long-standing assumption that phytoplankton distributions, along with environmental parameters, are homogenised by turbulence (Hutchinson, 1961; Siegel, 1998). Consequently, few studies use sampling intervals of less than a metre in the ocean. This exclusive focus on large scales, to achieve an understanding of ocean ecosystems, is consistent with current models that predict a bottleneck of homogeneity for phytoplankton distributions at scales of a few centimetres to tens of centimetres (Siegel, 1998). The

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bottleneck is implicitly assumed to block the cascade of effects from individual plankton interactions to larger scales by homogenising them to noise, making them irrelevant.

Surprisingly, the few studies of submetre distributions have found heterogeneous distributions, equivalent, in some cases, to the variation across the entire water column (Cassie, 1963; Derenbach et al., 1979; Mitchell and Fuhrman, 1989; Owen, 1989; Bjørnsen and Nielsen, 1991; Tiselius et al., 1994; Seymour et al., 2000). These findings expand the domain of microscale heterogeneous distributions into the mixed layer and build on established heterogeneity in thin layers at interfaces and density gradients (Cowles et al., 1993, 1998; Franks and Jaffe, 2001; McManus et al., 2003; Ryan et al., 2005). However, these studies are not representative, or general, because they were made at the sea surface, in strong density gradients or with a small sample size. Even so, these observations are supported by laboratory studies and models indicating that buoyancy, motility and reproduction can generate local phytoplankton heterogeneity (Kessler, 1986; Mitchell et al., 1990; Pedley and Kessler, 1990; Villareal et al., 1999; Young et al., 2001). A model for spatial asymmetry in microplankton birth and death suggests that individual cell processes can drive large scale patch production (Young et al., 2001), and other models suggest that regular patch spacing, even in noisy, nonlinear systems, may have the potential to spatially and temporally sychronise food webs (Ranta et al., 1997; Blasius et al., 1999; Cazelles and Boudjema, 2001). For these concepts to be relevant to marine ecosystems, patches must occur at the scale where the homogeneity bottleneck is predicted.

2. Methods

To test the extent of ocean microscale heterogeneity, we measured *in situ* fluorescence distributions at 2 mm sampling intervals for eight profiles of a well mixed water column, and analyzed the data for the variation, extent of spatial asymmetry and presence of patterns. Fluorescence is considered an indicator of phytoplankton biomass because of the ubiquitous presence of fluorescent photosynthetic pigments. The normally arbitrary units used to measure fluorescence were calibrated with sodium fluorescein and pure chlorophyll *a*, and then adjusted so that the units were roughly equivalent to μg/l of chlorophyll *a* (Wolk et al., 2001, 2002, 2006). To minimise the masking of microscale distribution by macroscale features, such as strong pycnoclines and nutriclines, a well-mixed water column was chosen. Salinity, temperature, shear and fluorescence were measured off the Japanese coast in the Neko Sato Sea (34°10′N, 132°30′E) using a TurboMAP free-fall profiler. This device uses hexagonally arrayed blue LEDs to excite a volume of about 1 cm^3, 1 cm in front of a detector (Wolk et al., 2001, 2002, 2006). By synchronously flashing the LEDS at up to 256 Hz, high resolution fluorescence measurements are made. The water column was well mixed and actively turbulent (Yamazaki et al., 2006). In the presence of such activity, water movement over centimetres to metres is isotropic (Frisch, 1995). Consequently, local fluorescence peaks are likely to be quasi-spherical patches rather than extensive layered sheets and we refer to these peaks in our data as patches.

3. Results and discussion

The overall water column was mixed, but the microscale profiles (Fig. 1) showed considerable structure, particularly with shear, that indicate a dynamic upper 65 m of the water column. Individual fluorescence patches, approximately 10 cm wide, were common and markedly asymmetrical, with upper patch boundaries usually marked by a rapid fluorescence increase and lower patch boundaries marked by slow declines (Fig. 2). This positive skew, relative to a local maximum, was observed throughout the profiles (Fig. 3A) with a mean maximum skew for the 8 profiles of 2.84 (±0.22, 95% CI) on a baseline of 0.16±0.11 ($\bar{x}$±SD). Patches were also usually leptokurtic, with the maxima for the 8 profiles having a mean of 9.60±1.70 on a baseline of −0.71±0.01. Patches became platykurtic for short sections (Fig. 2B, bottom line). The distance between patches was periodic over tens of centimetres (Fig. 2B) to the entire length of the profile (Fig. 3B). Sometimes complex distributions were evident. In one section (top, Fig. 2B) 10 patches were distributed as mirror images around 1 central patch (top, Fig. 2B). In other sections, regularly spaced patches showed a steady decrease or increase in amplitude (middle, Fig. 2A and B) or a change in frequency (middle and bottom, Fig. 2a and b). These patches do appear limited by physical conditions. When shear was high chlorophyll *a* intensity was low, indicating dispersal of these structures (Fig. 4).

The observed patch distributions are not due to sampling error or artifact of the falling profiler. The evidence for this is that patches showed variable skew and kurtosis and symmetric or negatively skewed patches occurred at low frequency in the profiles. Similarly, the sporadic nature of mirror imaging (top, Fig. 2B) makes it difficult to explain as systematic bias. Moreover, only

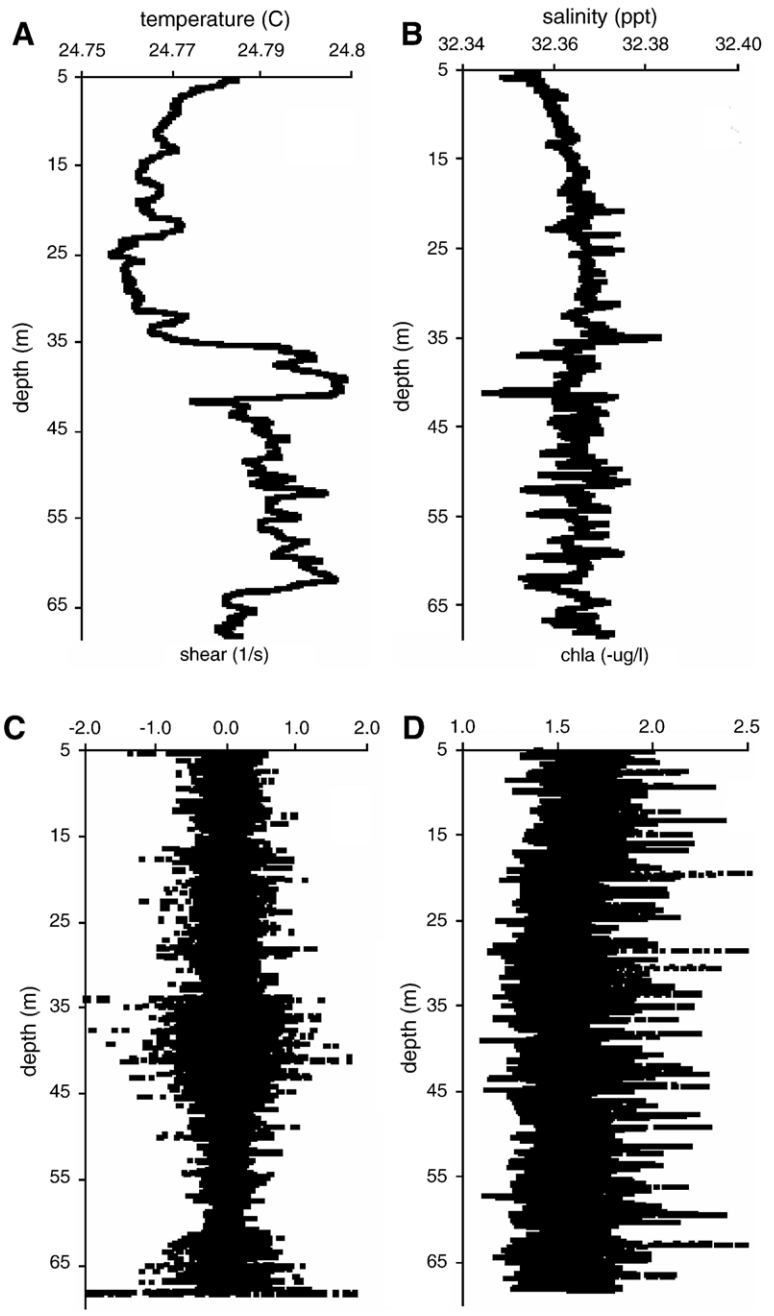

Fig. 1. Representative vertical profiles of temperature (A), salinity (B), shear (C) and chlorophyll *a* as estimated from fluorescence (D). The physical factors indicate a dynamically mixed upper water column. Note, fluctuations around the mean for salinity and shear are symmetrical, whereas they are slightly asymmetrical for temperature and highly asymmetrical for chlorophyll *a*.

changes of less than 5 points were determined to be noise for the fluorescence signal. We know of no solely physical mechanism that generates predominately positively skewed and leptokurtic patches. That leaves the biological process of motility, or combination of processes, such as sinking and aggregation, to explain the patch structures. These processes depend on biological properties, such as size, buoyancy, abundance, swimming speed and shape, all of which are taxa specific. These properties, combined with the presence of a uniform *in vivo* background fluorescence, suggest that particular groups of phytoplankton are concentrated

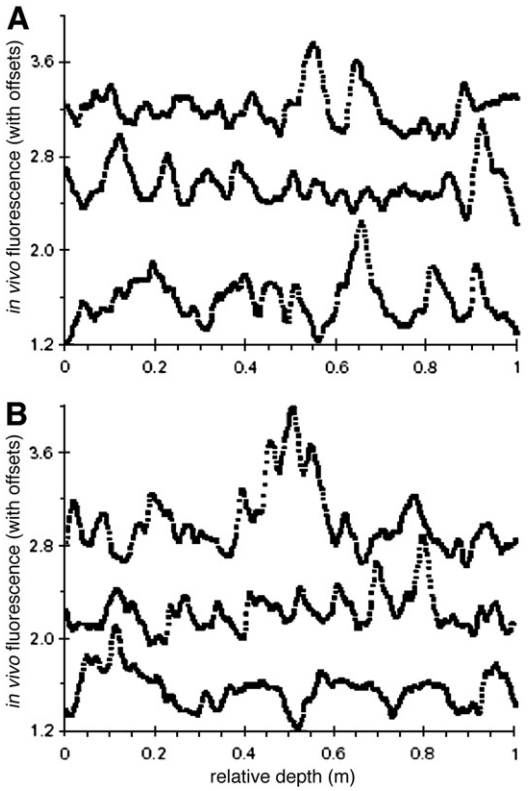

Fig. 2. One metre segments from 1 profile showing fluorescence microstructure. Similar patterns were seen throughout the eight profiles. (A) The top line shows two isolated peaks. The lower two lines are sequential and show slow attenuation of the signal, followed by a rapid increase in amplitude and frequency. (B) The top line shows mirror symmetry of peaks around a central peak. The peak symmetry extends outward for 3 to 4 peaks in each direction, including a pair of low, broad peaks. The middle segment shows evenly spaced peaks of increasing amplitude. The bottom segment is platykurtic and shows variation at a different frequency than the other segments. Each dash is one measurement. The top two segments in each graph have had 1.4 and 1 units (A) and 1.4 and 0.6 units (B) added to their original values. The added values were chosen to offset the lines so they did not overlap. From the top to bottom segments, 0 on the *x*-axis represents 7.0, 32.2, 33.2, 62.8, 44.0 and 66.9 m depth.

during an individual patch's lifetime. The lifetime is critical to the ecological relevance of these patches, given that some models suggest that associations among plankton last only a few seconds (Mitchell et al., 1985).

Four independent estimates below indicate that patch lifetimes are about 10 min. This is a sufficient time for patches to be areas of grazing, nutrient competition and infection. The highly intermittent nature of turbulence, however, means that only a small proportion of a turbulent ocean contains the most destructive eddies (Frisch, 1995; Jiménez, 1997; Seuront et al., 2001). We propose that patches form in quiescent parcels of seawater between rare but destructive high-shear parcels of seawater. This hypothesis is supported by Fig. 3, where the homogeneous fluorescence background occurs at the highest shear, and the maximum fluorescence signals occur at the minimum shear. The intermittency of turbulence means that some seawater parcels remain quiescent for much longer than the patch formation time. We propose that multiple patch patterns of regular spacing have time to develop in these regions (*e.g.* middle, Fig. 2B). Regular interpatch distance may be an important parameter in determining the effectiveness of grazing and the ability of infections to spread (Suttle, 1992; Tiselius, 1992). Furthermore, the mirroring and progressive amplitude changes (Fig. 2) suggest that adjacent patches are interdependent for position and

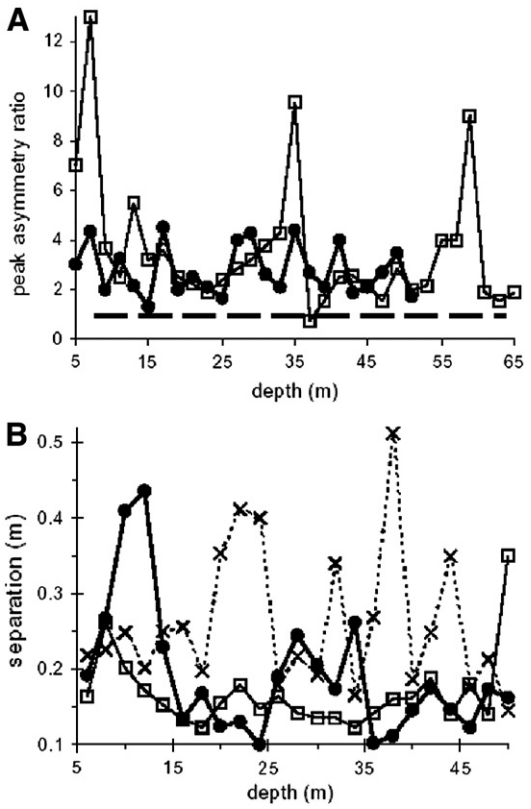

Fig. 3. Quantification of peak symmetry and separation over entire profiles in 2 m sections. For the upper panel, peaks were counted as positively skewed if the slope of the right (deep) side was less than that of the left (shallow) side. The heavy, dashed line indicates where positively and negatively skewed peaks are equally abundant. Negatively skewed peaks were present in all 2 m sections, but were only more abundant in one section. For the lower panel, the distances between peaks greater than 0.3 units were measured and the measurements grouped into 2 m sections. Changes in separation with depth were significant for all 3 profiles (table-wide $p<0.05$, one way ANOVA after sequential Bonferroni (Rice, 1989) for separations greater than 0.1 m). The same profiles for A and B are indicated by matching symbols.

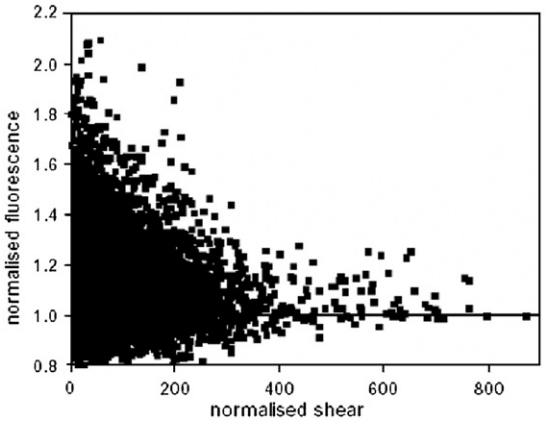

Fig. 4. Fluorescence as a function of shear. Both axes are normalised by the quietest section of the profile. For shear, this is the noise level of the sensor, $du/dz=0.05\ s^{-1}$. For fluorescence, this is the background level of approximately 1.1, well above the noise level of the sensor, which is <0.05. The horizontal black line indicates the maximum noise level for fluorescence, which corresponds to the maximum shear values.

amplitude. The local regular spacing (Fig. 2) and variation of this spacing over vertical distances of tens of metres (Fig. 3) indicates biological and physical processes may connect the patches in space or time over many metres. Preferential feeding by copepods on distinct growth stages and phytoplankton concentrations (Tiselius, 1992; Russel et al., 1992) become explainable and relevant *in situ* if there are opportunities to make choices on locally regular food abundance distributions. Segregated patch cascades would make such behaviour particularly relevant to copepod grazing dynamics.

To our knowledge, this is the first description of the structure and anatomy of microscale fluorescence distributions over a significant portion of the water column. At distances of centimetres, a seascape more complex than previously imagined exists. Richer and poorer areas occur at regular intervals and are possibly segregated, not only by species but also by physiological state. Such segregation may be a previously unappreciated, fundamental character of marine ecosystems that links microscale interactions with large scale processes. The existence of microscale phytoplankton patches bring seascape topography to a level of complexity close to that found in terrestrial ecosystems.

4. Patch lifetime estimates

4.1. Skew based lifetime estimate

We take the minimum time for skew to form as L/u, where L is ~1 cm (Fig. 2) and u is the sinking speed $2a^2g\Delta\rho/9\eta_e$, where a is the cell radius (25 μm), g is gravitational acceleration, $\Delta\rho$ is excess density (~0.05 g/cm^3) and η_e is the effective dynamic viscosity (0.01 cgs). This gives a minimum formation time of 147 s.

4.2. Aggregation based lifetime estimate

From previous work (*e.g.* Kiørboe, 1997) on the increase in the volume of aggregates we find the patch growth

$$L_t = L_0\left[e^{\alpha[7.8\varphi(\varepsilon/\nu)^{1/2}/\pi]t}\right]^{1/3} \quad (1)$$

where L_t and L_0 are the patch diameters at time 0 and t, α is the stickiness coefficient (0.5),ϕ is the volume-concentration of cells ($\phi=(4/3)\pi r^3C_0$, where r is phytoplankton cell radius, 25×10^{-6} m, and C_0 phytoplankton cells concentration, 5×10^{12} cells m^{-3} (Kiørboe, 1997)), ν is kinematic viscosity (2.5×10^{-6} m^2 s^{-1}) and ε is dissipation (1×10^{-7} m^2 s^{-3}). Using the stated values gives a patch lifetime of 700 s.

4.3. Turbulence based lifetime estimates

Turbulence sets an upper limit to patch lifetime. Patches may be destroyed by individual Kolmogorov eddies, local mixing at the energy containing time scale, or convective instability of part or the entire mixed layer. The limit for the Kolmogorov eddies is $T_k=(\nu/\varepsilon)^{1/2}=3$ s. However, the size of these eddies is $L_k=(\nu^3/\varepsilon)^{1/4}=0.002$ m, so that they are too small to mix an entire patch. Furthermore, intermittency means that the swarms of these eddies necessary to destroy a patch in this time are rare, leaving most patches unaffected. In contrast to this local affect, the entire flow field changes after $T_e=L/q$, where we assume the length scale, L, to be between 1 and 10 m, and derive q from $\varepsilon=q^3/L$ to give $T_e=217$ to 1000 s. Finally, from the Ozmidov scaling argument, the overturning time is simply the inverse of the buoyancy frequency, in this case 0.001, so the time scale is 1000 s.

5. The concept of patch patterns

Combining the estimated patch life times of 100 to 1000 s with the mixing evident in the physical parameters (Fig. 1) and frequency distributions of patch intensity and separation (Fig. 5) permits the formation of an overall picture of what these patches might look like and the role they might play in plankton ecology. The patches last on the order of

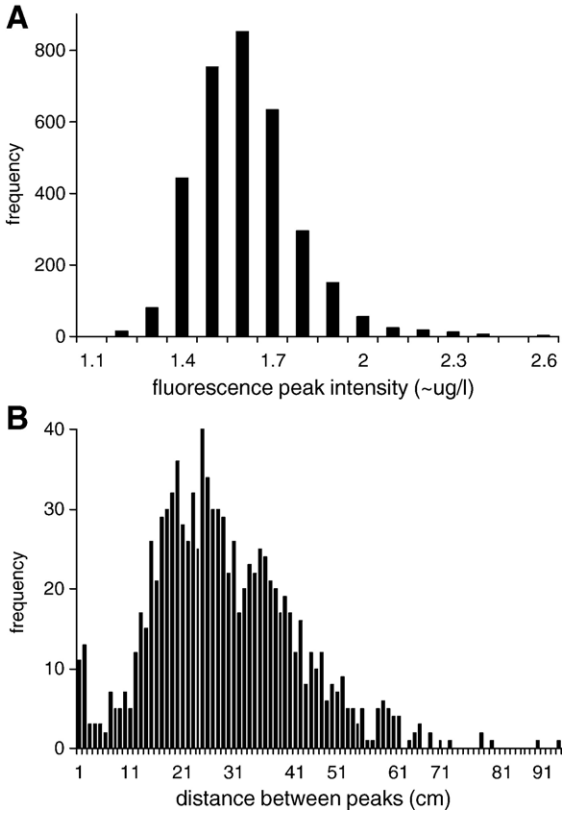

Fig. 5. The distribution of peak intensities (A) and the distance between these peaks (B). Changes were counted as peaks if they rose and fell more than 0.1 μg chl*a*/l and if they consisted of more than 5 points. The distance between peaks was measured as the distance between the center of one peak and the center of the next peak. Both distributions are skewed slightly, with the intensity distribution dropping off more rapidly than the distance distribution. The increased frequency at peak distances of 1 and 2 cm (B) appeared due to oscillations around the cutoff of 0.1 μg chl*a*/l.

10 min and are a few tens of centimetres in vertical extent. The strong mixing in the water column and the well known isotropic nature of turbulence at this scale suggests that the patches are of limited spatial extent in the lateral directions we did not measure. The patches described here appear distinct from those described as thin layers (McManus et al., 2003; Ryan et al., 2005). Their dispersal at high shear (Fig. 4) shows that they have less structural integrity than particles or marine snow, suggesting that they might range from phytoplankton in polymer matrix hotspots to motility driven clusters. While the lateral extent and patch generating mechanisms need further investigation, there is enough information to describe these as patches that while ephemeral may represent important structures for the survival of individual plankton and for linking individual behavior to larger scale oceanographic processes.

As with the profile pattern, the 2- and 3-dimensional patterns will be complex and appear nearly space filling. Here we present a pair of possible 2-dimensional schematics (Fig. 6). We created complex patterns because chlorophyll *a* gradients, unlike temperature and salinity, can increase in steepness as they are mixed due to internal generation and loss of chlorophyll *a* from reproduction, colony formation, grazing and lysis. These schematics should not be viewed in anyway as definitive, rather the challenge is to correct them and develop a more accurate picture of static distributions and dynamics at this scale.

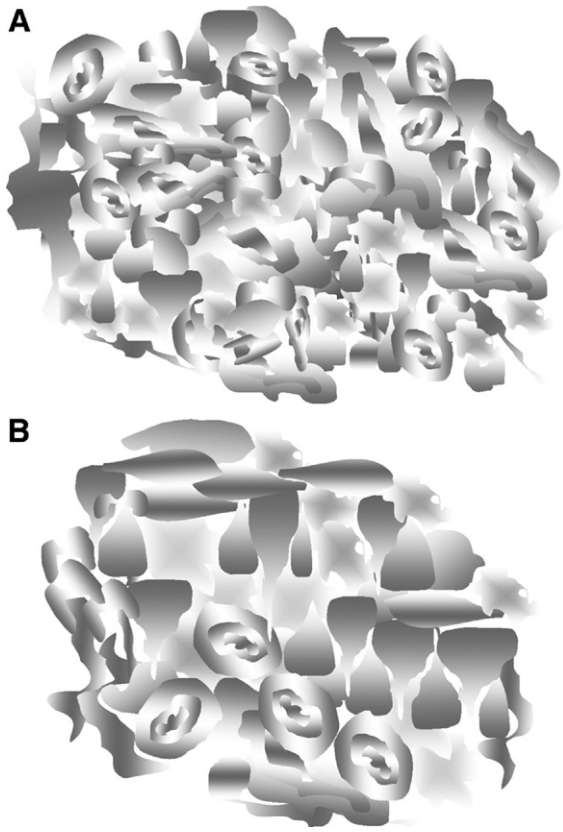

Fig. 6. Conceptual 2-dimensional distribution of phytoplankton patches under conditions of high shear that produces patterns only over short distances (A) and under conditions of reduced shear where patterns occur over shorter and longer distances (B). In (A) there are frequent interruptions of biologically generated patterns. In (B), biologically generated patterns, such as positive and negative vertical migration, rheotaxis, grazing and reproduction, occur at larger scales and are less frequently interrupted than in (A). The top to the bottom of each schematic is meant to be on the order of 1 m. White represents a hypothetical uniform background.

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