smallest size. It is formed by a gradual deformation of an $\eta$-size region with an initially uniform concentration. The shock contribution to the moment, $\langle \delta^2 \rangle = \int \text{d}x \langle \delta(y) \delta(y') \rangle \propto \text{Inf}[\lambda(t)^{-1}]$, contains a logarithm that is of order unity in our case. Therefore, we neglect shocks and consider fluctuations with $|\eta| < \eta^*$. The smallest size of the region evolves as $\eta = \eta^* \exp[\lambda(t)]$, where $\lambda^* = \lambda$ is the most negative Lyapunov exponent estimated as $\lambda(t) = \int \text{d}x \langle \delta^2 \rangle \delta \tau' \left( \frac{dx}{\delta} \right)$. Therefore, concentration fluctuations accumulate during the time $\text{Inf}[\lambda(t)]$. Because it is equal to the droplets' frame and the contribution of each cluster to the spatial average is proportional to its volume $\text{Inf}[\lambda(t)]$, we obtain:

$$\begin{align*}
\left( \langle \delta^2 \rangle = \langle \eta^2 \rangle \right) & \propto \int \frac{\text{d}x}{\delta} \langle \delta^2 \rangle \delta \tau' \left( \frac{dx}{\delta} \right) \\
& = \langle \eta^2 \rangle \exp \left[ -\frac{\langle \delta^2 \rangle}{\langle \delta \rangle} \langle \delta \rangle \right].
\end{align*}$$

(5)

where we assumed that $\ln(\eta^2) / |\lambda^*| \eta^* = \langle \eta^2 \rangle / |\lambda^*| \eta^*$. The higher terms of the cumulant expansion cannot be parametrically larger than the estimate (5) since they contain integrals estimated as $\langle \eta^2 \rangle \langle \delta \rangle \text{Inf}[\lambda(t)^{-1}]$, for $m \geq 1$, and both the correlation time $\tau_0$ and $\tau$ are less than $|\eta^*|^{-1}$ in the integration domain. Moreover, if $\langle \tau^2 \rangle / \langle \tau \rangle^2 \eta^* = \langle \eta^2 \rangle / |\lambda^*| \eta^*$, then equation (5) is correct not only parametrically but also numerically. To evaluate $\alpha$ we express it via the single-time PDF $P(\eta)$:

$$\alpha = \left( \tau = \frac{\eta^*}{|\lambda^*|} \right) \frac{\text{d}P(\eta)}{\text{d}\eta}. \quad \text{(6)}$$

To relate $P(\eta)$ to $P(\hat{\eta})$ measured experimentally we note that $\tau \sim \tau_0$ for $\tau_0 = \tau^{-1} \min(1, \eta^*)$ so that $P(\eta) = P(\eta^*)$ there. At $\tau > \tau_0$ the fluctuations of $\hat{\eta}$ contributing to $P(\hat{\eta})$ have $\tau \approx \tau$ and can occur at any moment within $\tau$. The extrapolation formulas at $\tau_0$ are $P(\eta^*) = (1 + \tau^2 \eta^2) P(\eta^*) = (1 + \tau^2 \eta^2) P(\eta^*) = \alpha \tau^2 \hat{\eta} \eta^* \alpha \tau^2 \eta^*$. Therefore, $\alpha$ is the maximum of $\alpha$ for any $\hat{\eta}$ that satisfies $\hat{\eta} \sim \tau_0$. Our theory is valid as long as $\text{Inf}[\lambda(t)] \eta^* < 1$.

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set comprised 6,339 seawater samples collected from an average of 9 to 10 depths in the photic zone of 656 hydrocasts. Although large, this data set lacked any winter measurements.

These data sets provide a clear delineation of phytoplankton variability in the ocean afforded by thousands of measurements. In a plot of phytoplankton abundance against chlorophyll biomass, the boundaries and internal structure of the data domain are indicated by colour-coded density regions (Fig. 1a). A polygon to encompass the data is given by the unit contour line, which excludes apparent outliers. This polygon has two rising edges: the bottom edge was defined by spring phytoplankters, whereas the top edge was defined by autumn phytoplankters. Large cells were more prevalent in spring whereas small cells were more so in autumn. The polygon also has a falling top edge such that above approximately 0.5 mg chlorophyll per m$^2$, maximum cell abundance decreased with increasing biomass, indicating the importance of large cells. This transition level of biomass may be the maximum potential for the picoplankton ($<2\mu$m) component of the community. At higher levels of photoautotrophic biomass, a substantial contribution is expected from the microphytoplankton, which were not counted. However, the upper boundary of the polygon would be largely unaltered because microphytoplankton in these waters, mainly diatoms and dinoflagellates, occur at concentrations between 1 and 1,000 cells ml$^{-1}$, which are too low to make a significant difference.

The structure of flow cytometric signatures for individual samples can be expressed by an index of so-called cytometric diversity. In this approach, the classification of phytoplankton is based not on taxonomy, but on ataxonomic categories in the bivariate biooptical domain of cell size and chlorophyll content defined by flow cytometric light scatter and red fluorescence. As such, cytometric diversity indicates richness in physiological as well as genetic variations. The index of cytometric diversity is calculated as Hill’s diversity number of order one; in other words, it is the exponential Shannon–Wiener index of the cytometric categories (exp $H'$). It is a measurement embodying the ideas of richness and evenness that define the uncertainty of an organism sampled at random; it is also a measurement of widespread use in phytoplankton ecology.

In the northwestern North Atlantic, the scatter plot of cytometric diversity against phytoplankton abundance filled a triangular polygon (Fig. 1b), indicating maximum diversity at an intermediate abundance of about 2,000 cells ml$^{-1}$. Phenomenologically, maximum diversity was a balance between richness and evenness. As more cells appeared in the community, diversity increased because new categories were added. However, as even more cells appeared, they were added to existing categories giving them dominant status, thus decreasing evenness and diversity.

A striking pattern was revealed in the manner in which different size classes were related to the total standing stock of chlorophyll a biomass (Fig. 2a). In the range of chlorophyll from about 10 to

![Figure 1](image1.png)

**Figure 1** Range of phytoplankton variability in the northwestern North Atlantic Ocean.  
**a.** Phytoplankton abundance versus chlorophyll concentration on a volumetric basis.  
**b.** Cytometric diversity$^d$ versus phytoplankton abundance. Samples were collected by Niskin bottles from depths of 0–100 m. The geographic distribution of the samples ($n = 6,339$) was 10% ARCT, 11% BPLR, 14% GFST and 65% NWCS. Contour levels indicate the number of overlapping data points in a grid region; the colour code indicates density, $H'$, Shannon–Wiener index.

![Figure 2](image2.png)

**Figure 2** Relationship of phytoplankton abundance to biomass and mean cell mass.  
**a.** Phytoplankton abundance versus chlorophyll concentration on an areal basis ($n = 656$). Picophytoplankton ($<2\mu$m, blue triangles), small nanophytoplankton (2–10 $\mu$m, yellow squares) and large nanophytoplankton (10–20 $\mu$m, green circles) were classified by reference to forward light scatter. Areal values were calculated by trapezoidal integration of volumetric values from 0 to 100 m.  
**b.** Phytoplankton abundance on an areal basis versus cellular carbon mass. Cell carbon was calculated from cell volume, which was based on the mean equivalent spherical diameter of the phytoplankton assemblage. The assemblage was an abundance-weighted average from 0 to 100 m depth. The line is the model II regression $\log N = 11.91 - 0.78\log M_{C}$.  

$\log N = 11.91 - 0.78\log M_{C}$.
1,000 mg m\(^{-2}\), a decrease in picoplankton (<2 \(\mu m\)) was mirrored by an increase in large nanoplankton (10–20 \(\mu m\)); however, small nanoplankton (2–10 \(\mu m\)) remained relatively invariant throughout. Here, the picoplankton were primarily *Synechococcus* cyanobacteria and small eukaryotic algae. There were no indications of *Prochlorococcus* cyanobacteria on the Scotian shelf or the Labrador Sea. The small nanoplankton were rich in 19-hexanoyloxyfucoxanthin, indicating prymnesiophytes. The large nanoplankton were rich in fucoxanthin, indicating primarily diatoms but including other algae as well (Bowman *et al.*, manuscript in preparation). It is widely held that marine phytoplankton communities are assembled by adding larger cells to a relatively uniform background of smaller cells\(^{11,14,15}\). The results here indicate that this uniform background is in fact the small nanoplankton. As phytoplankton communities grade from low to high biomass, there is a reduction in picoplankton, an increment in large nanoplankton, and no apparent net change in small nanoplankton.

These systematic patterns in the different size groups lead to phytoplankton communities that conform to an apparently universal relationship between population density and organism size\(^6,7\). The principles of allometric scaling\(^6\) proceed from a large body of observations that relate metabolic rate \((B)\) to body mass \((M)\) according to the 3/4 power law, \(B = B_0M^{3/4}\), where \(B_0\) is a proportionality coefficient. From this, the allometric basis for population density of terrestrial plants can be interpreted as follows\(^7\). In individual plants, the rate of resource use \((Q)\) is proportional to \(B\), and thus \(Q \propto M^{3/4}\). The number of individuals per unit area \((N)\) that can be supported by a rate of resource supply \((R)\) is \(N = RQ^{-1}\).

**Methods**

Chlorophyll \(a\) was measured in acetone extracts of particulate matter collected on Whatman GFF filters using a Turner Designs fluorometer. Phytoplankton in aliquots...

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**Figure 3** Influence of water-column stability on phytoplankton abundance (a) and cytometric diversity (b) \((n = 658)\). The stratification index is the seawater density \((\rho)\) difference normalized to the depth \((z)\) difference, which was about 90 m in most cases. Cytometric diversity was calculated as the abundance-weighted average from 0 to 100 m. Phytoplankton size classes are colour coded as in Fig. 2a.
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Coping with smooth eye movements in three-dimensional space by frontal cortex

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Through the development of a high-acuity fovea, primates with frontal eyes have acquired the ability to use binocular eye movements to track small objects moving in space. The smooth-pursuit system moves both eyes in the same direction to track movement in the frontal plane (frontal pursuit), whereas the vergence system moves left and right eyes in opposite directions to track targets moving towards or away from the observer (vergence tracking). In the cerebral cortex and brainstem, signals related to vergence eye movements—and the retinal disparity and blur signals that elicit them—are coded independently of signals related to frontal pursuit. Here we show that these types of signals are represented in a completely different way in the smooth-pursuit region of the frontal eye fields. Neurons of the frontal eye field modulate strongly during both frontal pursuit and vergence tracking, which results in three-dimensional cartesian representations of eye movements. We propose that the brain creates this distinctly different intermediate representation to allow these neurons to function as part of a system that enables primates to move objects moving in three-dimensional space.

In two monkeys, we recorded the activity of 225 neurons that was modulated during frontal pursuit and/or vergence tracking of laser spots projected onto a vertical or horizontal screen (Methods). Of 122 neurons tested during both frontal pursuit and vergence tracking, 80 (66%) responded to both (three-dimensional 3D) tracking. Thirty (25%) responded only during frontal pursuit and 12 (9%) responded only during vergence tracking. Of the 92 neurons that responded during vergence tracking, 39 were activated during divergence (Fig. 1a), 45 during convergence (Fig. 3a, f) and 8 during both (data not shown). The neuron shown in Fig. 1a–d was activated strongly as the monkey tracked a target moving away from him (Fig. 1a) and more weakly during downward pursuit (Fig. 1d). Because the horizontal screen used to present targets moving in depth was at nose level, divergence eye movements were accompanied by small (0.8°) upward eye movements. This combined motion that was required during vergence tracking could not explain the increased discharge of this neuron during divergence, because it was activated during downward pursuit.

Similar arguments could be applied to the 36 neurons that had no response to vertical pursuit, or a response in the wrong direction, to account for their observed modulation during vergence tracking. For neurons whose vertical pursuit sensitivity was in the correct direction to contribute to their modulation during vergence tracking, the contribution was too small to account for the modulation observed during vergence tracking. Figure 2a shows this for a divergence plus upward pursuit neuron whose eye velocity sensitivity was at 0.3, 0.5 and 1.0 Hz was much smaller during frontal pursuit than during vergence tracking.

Figure 2b plots the relationship between vergence-tracking and frontal-pursuit (combined horizontal, vertical) sensitivities for five groups of neurons. Sensitivities varied widely with a tendency for

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