

Mesoscale vortices and the paradox of the plankton

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Coexistence of competitive species is severely limited by the availability of resources and the characteristics of the environment. In particular, the so-called ‘competitive exclusion principle’ states that, at equilibrium, the number of coexisting species cannot be larger than the number of resources for which they compete. However, many *in situ* observations have revealed prolonged coexistence of a large number of competitive plankton species, a phenomenon known as ‘the paradox of the plankton’. Here we investigate this problem and show that ocean mesoscale vortices generate transport barriers and incomplete horizontal mixing, allowing for a prolonged survival of the less-fit species, even for fully homogeneous resource distributions. In such a situation, the temporarily less-fit plankton species are protected from competition by the action of the vortices.

Keywords: plankton; coherent vortices; geophysical turbulence

1. INTRODUCTION

In homogeneous and well-mixed environments, species that compete for the same resources cannot coexist for long time-periods. This observation is formalized by the so-called ‘competitive exclusion principle’ (Hardin 1960; Armstrong & McGehee 1980), which states that, at equilibrium, the number n of coexisting competitive species cannot be larger than the number k of limiting resources. Even if the populations can randomly diffuse over the whole available domain (Okubo 1980), the species characterized by slower multiplication and/or lower survival rate are rapidly eliminated until $n \leq k$.

The communities composing the phototrophic phytoplankton are an example of this type, as they compete for a small number of potentially limiting resources, such as diluted inorganic materials and light, particularly in the summer (e.g. Phillips 1973). By contrast, many *in situ* observations have revealed prolonged coexistence of a large number of competitive plankton species. This phenomenon, known as ‘the paradox of the plankton’, was formulated by Hutchinson almost forty years ago (Hutchinson 1961).

In the past, several possible solutions to the plankton paradox have been proposed, including spatial and temporal heterogeneity in the physical or biological environment, incomplete mixing, and non-stationary (periodic or chaotic) behaviour in the plankton dynamics (Richerson *et al.* 1970; Levins 1979; Atkinson & Shorrocks 1981; Powell & Richerson 1985; Sommer 1985; Muratori & Rinaldi 1989; Tilman 1994; Truscott & Brindley 1994; Huisman & Weissing 1999; Huisman *et al.* 1999; Scheuring *et al.* 2000). In particular, externally imposed or self-generated spatial segregation has been recognized as a possible reason for the coexistence of competitive species (Ives & May 1985; Britton 1989; Hassel *et al.* 1994).

In this work, we examine a scenario where horizontal mesoscale turbulence, characterized by the presence of coherent vortices, influences the fate of competitive

plankton populations. The vortices generate dynamic transport barriers and allow for prolonged survival of competitive species in an otherwise homogeneous environment. Clearly, vortices alone cannot assure an infinitely long plankton coexistence, as species trapped inside vortices will sooner or later come into contact with species outside, due to small-scale turbulent mixing and the finite lifetime of the vortices themselves. However, thanks to the shielding effect generated by the vortex cores, the less-fit plankton species can survive for several months, until environmental conditions (related, for example, to the marching of the seasons) become more favourable. Mesoscale features can also help to explain the different (but somehow related) issue of plankton patchiness (e.g. Denman & Platt 1976; Steele 1978), as discussed by Flierl & Davis (1993), Smith *et al.* (1996), Abraham (1998), and Spall & Richards (2000).

Long-lived coherent vortices do indeed permeate the world’s oceans, as revealed by both observation (Hooker & Brown 1994) and high-resolution numerical simulation (Chassignet 1992; Paiva *et al.* 1999). Vortices play an important role in the transport of material constituents and dynamic quantities across the ocean, and affect the overall distribution of eddy kinetic energy (Siegel *et al.* 2000). The flow model used here, known as quasi-geostrophic turbulence (Pedlosky 1987), is a simplified dynamical description of mesoscale ocean motions that is characterized by the spontaneous emergence of coherent vortices (McWilliams 1984, 1990; Babiano *et al.* 1987). Coherent vortices are spatially localized patterns in the vorticity field, with a long lifetime (hundreds of rotation periods). Most of the energy and vorticity of the system is concentrated in these vortices, which extend their influence over large distances (Bracco *et al.* 2000).

It is known that coherent vortices affect the dynamics of advected tracers in several ways. Vortices act as barriers to material exchanges between their cores and the external background turbulence, and enhance transport of constituents trapped in their interior (Elhmaïdi *et al.* 1993; Provenzale 1999). This impermeability induces strong inhomogeneities in the tracer distributions over

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long time-scales. In particular, ocean eddies have been shown to trap plankton communities in their cores for periods longer than one year (Ring Group 1981).

Here we show that the presence of coherent vortices can slow down the selection process to time-scales that are long enough to allow for the survival of competitive phytoplankton species.

2. SIMULATED PLANKTON DYNAMICS

In the following, we adopt a mixed Eulerian–Lagrangian description of the turbulent dynamics and integrate the motion of plankton-carrying fluid elements in a flow representing the surface layer of the ocean. For simplicity, we consider only two passively advected plankton species that compete for a homogeneously distributed resource.

In our approach, vertical motions of the fluid elements are not allowed. Thus, the fluid patches considered here represent vertically integrated sample portions of the surface mixed layer, and the model dynamics describe large and mesoscale horizontal mixing by geostrophic turbulence.

The time integration of the model proceeds as follows. Each fluid element, labelled by j , is located at the position (X_j, Y_j) at time t . A generic fluid element contains two competitive phytoplankton populations, called A and B, that have concentrations $a_j(t)$ and $b_j(t)$, respectively. Note that both species can be present in the same fluid parcel.

The fluid elements are advected by a turbulent horizontal velocity field, $\mathbf{u} = (u, v)$, that is a function of space and time. The positions of the fluid elements evolve in time as

$$d\mathbf{X} = \mathbf{u}(\mathbf{X}, t)dt, \quad (1)$$

where $d\mathbf{X} = (dX, dY)$ is the infinitesimal increment in the position of the fluid parcel and dt is an infinitesimal time increment. We keep a differential notation instead of the more standard time derivative because the velocity field can be a stochastic variable.

In the model, we make the simplifying assumption that the concentrations a_j and b_j can change only at specified time intervals (e.g. once a day due to the diurnal cycle), when the two species compete and their concentrations change due to the different reproduction and survival rates. To practically implement the competitive dynamics, at the selected time intervals we evaluate the local concentrations of the two species on a spatial Eulerian grid, as obtained by averaging the concentrations carried by all the fluid elements that are inside a given grid cell with size ε , where ε defines the length of small-scale homogenization. This leads to the definition of two averaged macroscopic concentration fields $a_\varepsilon(x, y, t)$ and $b_\varepsilon(x, y, t)$, where (x, y) are the coordinates of the grid points (i.e. geographical coordinates on the ocean surface). The concentrations after competition are then given by

$$\begin{aligned} a'_\varepsilon &= \frac{\alpha a_\varepsilon}{\alpha a_\varepsilon + \beta b_\varepsilon}, \\ b'_\varepsilon &= \frac{\beta b_\varepsilon}{\alpha a_\varepsilon + \beta b_\varepsilon}, \end{aligned} \quad (2)$$

where α and β are the multiplication rates. Clearly, the species with the largest multiplication rate selects out the other one. The new concentration in each grid cell is then assigned to all the fluid elements contained inside that cell, simulating diffusion and homogenization on the scale of one grid cell. Note also that the total concentration in each grid cell and for each fluid element is normalized such that $a + b = 1$ at any time (however, the results remain qualitatively the same if $a + b$ is normalized to another constant or to a slowly decaying function of time, for example representing mortality).

In the model considered here, the annual cycle of planktonic ecosystems is not taken into account. In nature, this cycle leads to the creation of a mixed layer at the end of winter, followed by a phytoplankton bloom at the beginning of spring. Then, during summer and fall, phytoplankton growth is limited by the availability of nutrients, and inhomogeneities in the environment can dominate over bloom behaviour. In the present approach, the role of turbulence is tested on time-scales of at most six to nine months, corresponding to the period between two subsequent spring blooms.

Clearly, the model assumptions are very crude. The model, in particular, neglects sinking, incomplete vertical mixing, relative grazing and interactions between nutrient limitation and competition for light, even though those factors can have a major impact on the species compositions. However, the extreme simplification of this model allows for clear elucidation of the basic effects of horizontal mesoscale structures on phytoplankton coexistence.

3. THE FLOW MODELS

(a) *Geostrophic turbulence*

The equation that describes barotropic turbulence in the quasi-geostrophic approximation (see Pedlosky (1987) for a complete derivation) is

$$\frac{D\omega}{Dt} = \frac{\partial\omega}{\partial t} + \mathcal{J}[\psi, \omega] = D + F, \quad (3)$$

where D/Dt is the total advective derivative, $\mathcal{J}[\psi, \omega] = \partial_x\psi \partial_y\omega - \partial_y\psi \partial_x\omega$ is the two-dimensional Jacobian operator, ψ is the streamfunction and $\omega = \nabla^2\psi$ is relative vorticity. The velocity field $\mathbf{u} = (u, v)$ is given by $u = -\partial_y\psi$ and $v = \partial_x\psi$. The dissipative term D represents horizontal eddy viscosity and it provides a parameterization of both unresolved small-scale motions and large-scale friction (see below). The forcing F represents an energy input from large-scale motions.

Barotropic turbulence is characterized by a direct cascade of enstrophy (the integral of squared vorticity, \mathcal{Z}) towards small scales and by an inverse cascade of kinetic energy from small to large scales (Kraichnan 1967; Batchelor 1969). In this flow, a random initial vorticity field spontaneously evolves into coherent vortices that carry most of the energy and vorticity of the flow and dominate the dynamics (McWilliams 1984, 1990). Figure 1 shows a picture of the vorticity field after vortex emergence.

In the following, forcing is imposed at a given wavenumber k_r , keeping the energy at this scale fixed in time. Thus, inverse energy cascade is observed for

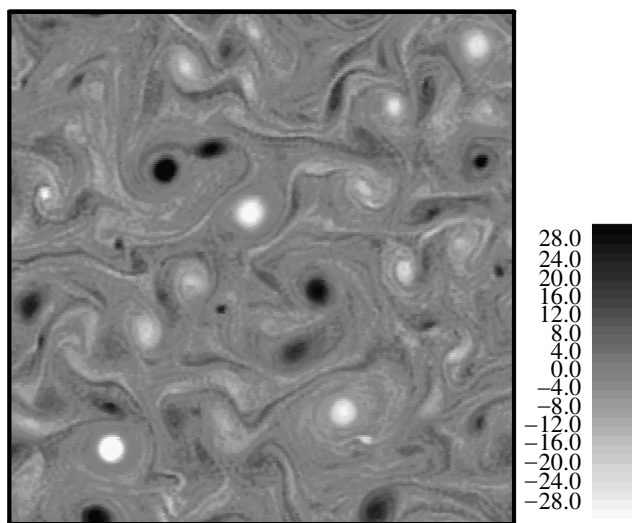


Figure 1. Vorticity distribution at the time when plankton-carrying fluid elements are released. The grey scale indicates relative vorticity.

$k < k_f$ and direct enstrophy cascade for $k > k_f$. With this type of forcing, vortices have a size close to the forcing scale. The dissipative term is given by the sum of two terms, $D = D_v + D_f$. Here D_v is a hyperviscous term acting at small scales, $D_v = -\nu \nabla^8 \nabla^2 \psi$ where ν is the viscosity coefficient, and D_f is a friction term, proportional to ψ , which acts at the largest scale to dissipate the energy piled up by the inverse energy cascade. Forcing and dissipation are balanced to give a statistically stationary turbulent flow. In this system, plankton-carrying fluid elements are advected by using equation (1).

Equation (3) is numerically integrated on a doubly periodic square domain with size $L = 2\pi$ by using a pseudo-spectral code with standard 2/3 dealiasing and 256^2 collocation points (see Canuto *et al.* (1987) for details of the numerics). The forcing wavenumber is fixed as $k_f = 10$, and dissipation and forcing are kept as small as possible to achieve a large Reynolds number. The time integration of the vorticity field is performed by a third-order Adams–Bashforth scheme. When the flow has reached statistical equilibrium between forcing and dissipation, 256^2 plankton-carrying fluid elements are uniformly released in the domain. The motion of the fluid elements is integrated by using a third-order Adams–Bashforth time integration scheme and a third-order spectral spline interpolator for a total time $T = 20$.

To obtain a physical estimate of the time- and space-scales of the model, we recall that the typical eddy-turnover time T_e in the ocean is about 8 days. In the present simulation, $T_e = \zeta^{-1/2} \approx 0.25$. Comparing the two values, we find that one adimensional time unit of the model corresponds to a physical time-span of one month. In physical units, the total integration time is thus $T \approx 20$ months. The physical length-scale can be determined by recalling that the typical forcing scale in the ocean is of the order of 50 km. Since $k_f = 10$ in the model, the physical size of the integration domain can be fixed as $L \approx 500$ km, and one grid spacing corresponds to about 2 km.

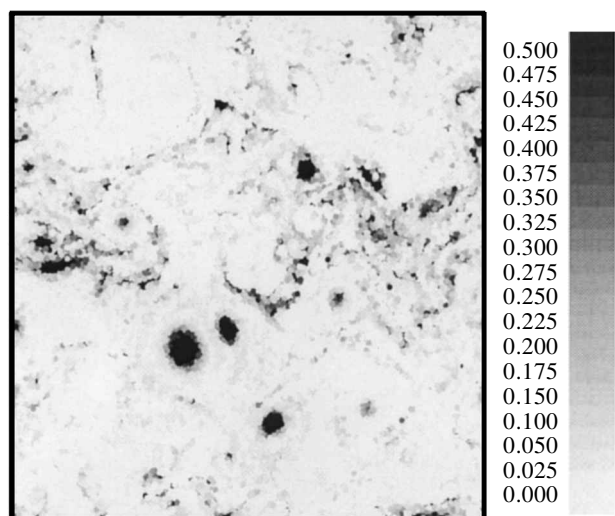


Figure 2. Distribution of $a_e(x, y, t)$ at time $t = 10 \approx 10$ months after release, as indicated by the grey scale. Black patches contain only species A; white patches are dominated by species B.

(b) *Random walk*

Together with vortex-dominated, self-consistent geostrophic turbulence, we also consider two standard homogeneous stochastic models (see Griffa (1996) for a review) in order to have test cases of plankton dynamics in unstructured turbulence. The continuous limit of these models leads to various forms of standard reaction–diffusion dynamics.

The first stochastic model we consider is a classic ‘random walk’, and it assumes that the tracer position is a Markov variable. The equation that describes the tracer motion can be written as

$$\begin{aligned} d\mathbf{X} &= \mathbf{u} dt, \\ d\mathbf{u} &= (\sigma^2/T_L)^{1/2} d\mathbf{w}. \end{aligned} \quad (4)$$

Here $d\mathbf{X}$ is the total displacement of the particle during the time dt , $d\mathbf{u}$ is the velocity increment, σ^2 is the velocity variance, T_L is the average Lagrangian integral time-scale and $d\mathbf{w}$ is a random increment extracted from a normal distribution with $\langle d\mathbf{w} \rangle = 0$ and $\langle dw_i(t) dw_j(t') \rangle = 2\delta_{ij} \delta(t-t') dt$, where the subscripts indicate vector components and $\langle \cdot \rangle$ indicates ensemble average.

The second model, usually referred to as an Ornstein–Uhlenbeck process, assumes that the particle position \mathbf{X} and the turbulent velocity \mathbf{u} are jointly Markovian. In this case, the advection equations become

$$\begin{aligned} d\mathbf{X} &= \mathbf{u} dt, \\ d\mathbf{u} &= -\frac{1}{T_L} \mathbf{u} dt + (\sigma^2/T_L)^{1/2} d\mathbf{w}, \end{aligned} \quad (5)$$

where \mathbf{u} is drawn from a Gaussian distribution with zero mean and variance σ . This stochastic process has been shown to provide an approximate description of the second-order particle statistics in the upper ocean (Griffa 1996), although it does not capture the effects of vortex dynamics (Pasquero *et al.* 2000).

For consistency, we fix the values of σ^2 and T_L in the stochastic models equal to those obtained from the

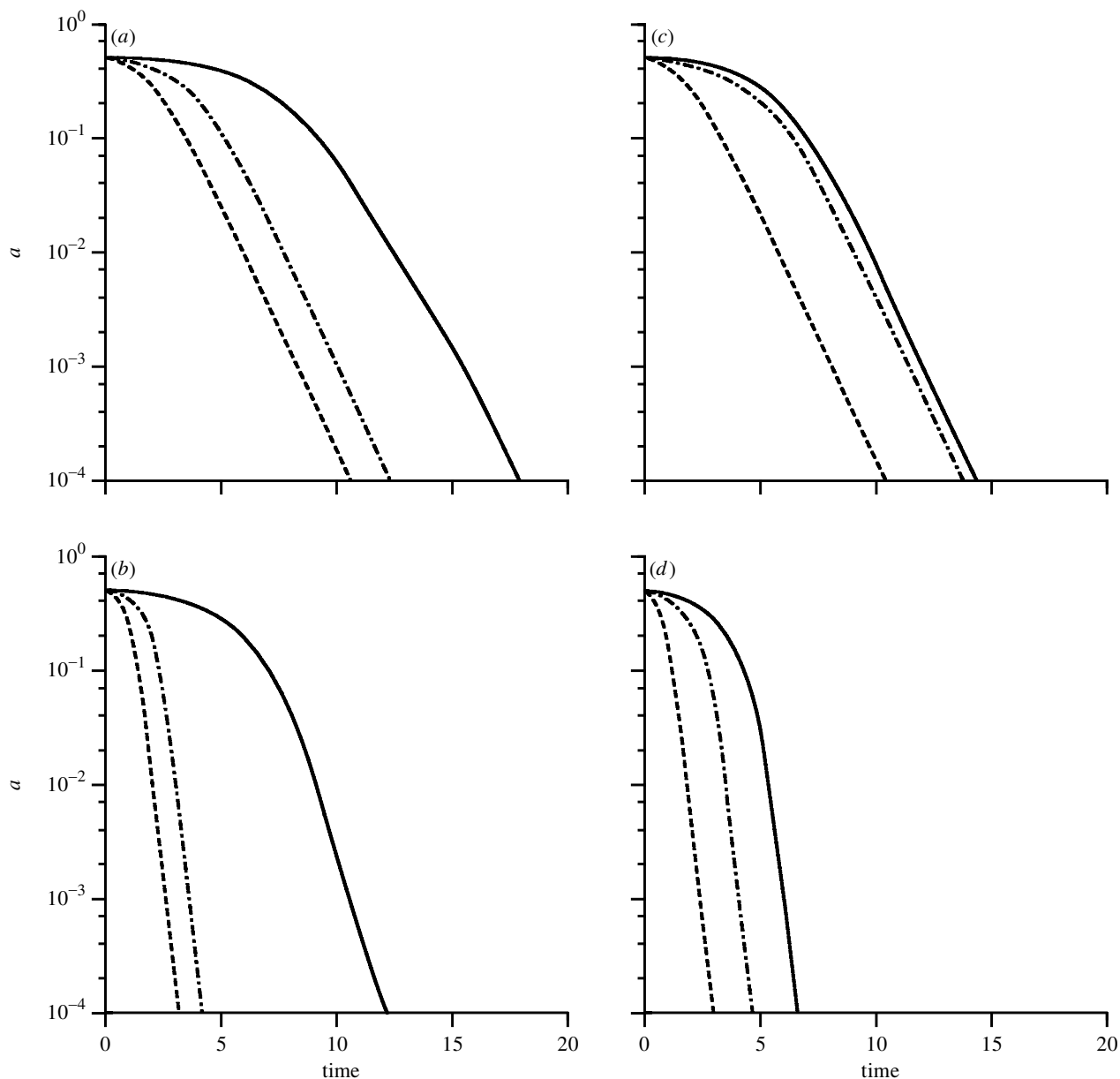


Figure 3. Time evolution of the average concentration of species A for advection: by geostrophic turbulence, equation (3) (solid line); by the Ornstein–Uhlenbeck process, equation (6) (dashed–dotted line); and by the Brownian random walk, equations (5) (dashed line). The values of the parameters are as follows: (a) $\alpha/\beta = 0.9$ and $\varepsilon = 1$ grid spacings; (b) $\alpha/\beta = 0.67$ and $\varepsilon = 1$ grid spacings; (c) $\alpha/\beta = 0.9$ and $\varepsilon = 2$ grid spacings; (d) $\alpha/\beta = 0.67$ and $\varepsilon = 2$ grid spacings.

gostrophic turbulence simulation. In particular, the average Lagrangian integral time-scale is defined as

$$T_L = \int_0^\infty R(\tau) d\tau, \tag{6}$$

where $R(\tau)$ is the ensemble-averaged Lagrangian velocity autocorrelation, i.e.

$$R(\tau) = \lim_{T \rightarrow \infty} \frac{1}{\sigma^2} \int_0^T \langle \mathbf{u}(t) \cdot \mathbf{u}(t + \tau) \rangle dt, \tag{7}$$

where the average $\langle \cdot \rangle$ is taken over the ensemble of fluid elements advected by the barotropic turbulent field.

4. RESULTS

In the following, we discuss the dynamics of the two competitive plankton populations A and B, advected by the different types of turbulent models described in § 3.

The competitive dynamics start with all fluid elements in $0 < x < L/2$ occupied by species A (here, $a_\varepsilon = 1$ and $b_\varepsilon = 0$ at $t = 0$) and elements in $L/2 < x < L$ occupied by B-type entities (here, $a_\varepsilon = 0$ and $b_\varepsilon = 1$ at $t = 0$). We choose the species A to be the competitively inferior one, i.e. $\alpha/\beta < 1$.

Figure 2 shows the concentration field $a_\varepsilon(x, y, t)$ at time $t = 10 \approx 10$ months for the case of geostrophic turbulence, with $\varepsilon = 1$ grid spacings (physically, this corresponds to diffusive plankton homogenization on

scales of about 2 km) and $\alpha/\beta = 0.9$. After several months, A-type entities are still concentrated inside the coherent vortices that were initially in $0 < x < L/2$ and in the vorticity filaments generated during vortex–vortex interactions. During this time, the vortices have moved around in the whole domain. Due to the strong vorticity gradients present on their edge, the vortices have acted as transport barriers, protecting the A-type weaker plankton present in their cores from competition with the other species. This, in turn, allows for a prolonged survival of the less-fit species.

By contrast, the less-fit species survives for a much shorter time when unstructured stochastic advection is considered. To provide a quantitative comparison of the different cases, in figure 3 we show the time evolution of the average concentration of A for different values of α , β and ε , for the three types of advection discussed above. In panels (a) and (b), ε is one grid spacing. The ratio α/β is (a) 0.9 and (b) 0.67. In panels (c) and (d), ε is set equal to two grid spacings, again with $\alpha/\beta = 0.9$ and 0.67. When tracers are advected by Brownian motion or by an Ornstein–Uhlenbeck process, the concentration of the species with the lower multiplication rate decreases rapidly, and the less-favoured plankton population is soon eliminated. After just a few months, the average concentration of A in the turbulent mesoscale flow is already much larger than for random advection. At $t \approx 10$ months, for random dispersion with no coherent vortices, the system is homogeneously occupied by B-type entities.

We performed several simulations, varying the homogenization range ε , the ratio α/β and the time interval between subsequent competition events, finding analogous results. For all values of α/β that we considered, the concentration of the population with the lower multiplication rate maintains a significant level for a longer time when it is advected by geostrophic turbulence. The value of the homogenization range ε is more critical, because the survival of the less favoured population is significantly shortened as ε grows beyond a few kilometres. All together, these results indicate that when small-scale horizontal plankton homogenization is confined below about 5 km and mesoscale advection is dominated by vortex dynamics, the less-fit species can survive over relatively long time-scales (about ten months) inside the coherent vortices.

5. CONCLUSIONS

In this work, we have studied the dynamics of different planktonic species that are in competition for the same resources, and we have explored the role of mesoscale vortices in the advecting flow. We have shown that coherent vortices in a turbulent environment can lead to strongly non-uniform spatial planktonic patterns and to prolonged survival of competitive species, preventing the less-fit species from being driven out completely during the most critical months. Because in real ecosystems the environmental conditions vary in space and time, a weaker competitor at a given location in one year can become the stronger one in the following year or in another place. Thus, competing phytoplankton, with the help of mesoscale vortices, can remain in non-equilibrium

coexistence on very long time-scales. On the contrary, horizontal dispersion by unstructured random walks with mixing-length step size with a homogeneous resource distribution is not able to sustain the great number of coexisting planktonic species observed in oceanic surface waters, leading to disappearance of the less-fit species on time-scales that are presumably shorter than those associated with the varying environmental conditions. This provides a further indication of the important dynamical role that coherent vortices play in the ocean.

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