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A model for resolving the plankton paradox: coexistence in open flows

ISTVÁN SCHEURING,* GYÖRGY KÁROLYI,† ÁRON PÉNTEK,‡ TAMÁS TÉL§ and
ZOLTÁN TOROCZKAI††,¶

**Department of Plant Taxonomy and Ecology, Research Group of Ecology and Theoretical Biology, Eötvös University, Ludovika tér 2, H-1083 Budapest, Hungary*

†Department of Civil Engineering Mechanics, Technical University of Budapest, Muegyetem rkp. 3, H-1521 Budapest, Hungary

‡Marine Physical Laboratory, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093-0238, USA

§Institute for Theoretical Physics, Eötvös University, P.O.Box 32, H-1518 Budapest, Hungary

††Department of Physics, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0435, USA

¶Centre for Nonlinear Studies and Theoretical Division, Los Alamos National Laboratory, Mailstop B258 Los Alamos, NM 87545, USA

SUMMARY

1. Recent developments in the field of chaotic advection in hydrodynamical/environmental flows encourage us to revisit the population dynamics of competing species in open aquatic systems.

2. We assume that these species are in competition for a common limiting resource in open flows with chaotic advection dynamics. As an illustrative example, we consider a time periodic two-dimensional flow of viscous fluid (water) around a cylindrical obstacle.

3. Individuals accumulate along a fractal set in the wake of the cylinder, which acts as a catalyst for the biological reproduction process. While in homogeneous, well mixed environments only one species could survive this competition, coexistence of competitors is typical in our hydrodynamical system.

4. It is shown that a steady state sets in after sufficiently long times. In this state, the relative density of competitors is determined rather by the fractal nature of the spatial distribution of the advected species, and by their initial conditions, than by their competitive abilities. We argue that two factors, the strong chaotic mixing along a fractal set and the boundary layer around the obstacle, are responsible for the coexistence.

Keywords: chaotic advection, environmental flow, fractal set, hydrodynamical flow, population dynamics

Introduction

The problem of coexistence of competing species is a classical question in theoretical ecology. In most natural habitats, numerous competing species are able to coexist, while generally only few resources (niches) limit these communities. This fact contradicts the classical theoretical and empirical studies predicting competitive exclusion of all but the most perfectly

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Correspondence: I. Scheuring, Department of Plant Taxonomy and Ecology, Research Group of Ecology and Theoretical Biology, Eötvös University, Ludovika tér 2, H-1083 Budapest, Hungary.
E-mail: shieazsf@ludens.elte.hu

adapted species for each limiting factor (Gause & Witt, 1935; Hardin, 1960).

This puzzle, originally presented by Hutchinson (1961), is most strikingly present in phytoplankton communities. Hutchinson asked the question: 'How is it possible for a number of species to coexist in a relatively isotropic or unstructured environment, all competing for the same sorts of materials?' To solve this so called 'paradox of the plankton', he put forward the idea that seasonal environmental changes prevent competitive exclusion in natural phytoplankton communities. Thus, the species in the community, at least on the time scale of ecological observation, are in non-equilibrial coexistence.

Since then, numerous investigations have reinforced the notion that many different mechanisms, including the spatial and temporal heterogeneity of habitat, predation, disturbance, coevolution etc., might increase the probability of competitive coexistence. Naturally, under the word 'competition', many different biological phenomena are collected together, which influence the coexistence of species in different ways. Thus, the original problem changed into finding the most relevant mechanisms which maintain diversity in particular situations (Connell, 1978; Huston, 1979; Wilson, 1990; Tilman & Pacala, 1993; Bartha, Czárán & Scheuring, 1997). Despite the lively debate in this field of ecology, there is now a consensus that climatic periodicities and fluctuations play the main role in causing species' persistence in phytoplankton communities (Gaedeke & Sommer, 1986; Reynolds, 1993; Sommer *et al*., 1993). Freshwater ecologists frequently argue that an intermediate disturbance (Connell, 1978) is the most adequate hypothesis for the explanation of high diversity in aquatic systems (cf. Reynolds, 1998). According to this view, the environmental fluctuations (e.g. wind blows and storms) disturb ecosystems in a spatially and temporally non-uniform manner. If this disturbance is neither too intense and frequent nor too weak and rare, the community behaves as a complex mosaic of different non-equilibrial subsystems. This qualitative argumentation is convincing and supported by microcosm (Gaedeke & Sommer, 1986) and field experiments (Reynolds, 1986 and references therein). However, to determine the relevant spatiotemporal scales of disturbance and community dynamics is still a great methodological challenge for ecologists (Collins & Glenn, 1997; Bartha *et al*., 1997).

Our aim here is to show that a pure hydrodynamical phenomenon, chaotic advection (Ottino, 1989; Jana, Metcalfe & Ottino, 1990; Aref, 1994), ensures a peculiar small-scale spatial heterogeneity that allows the coexistence of competing species. For phytoplankton populations, this provides a novel possibility for explaining coexistence. In fact, the mechanism proposed by us could also be a consequence of some intermediate disturbance. Frequent but moderate winds may drive the water sufficiently to generate chaotic advection, thus supporting coexistence.

Our model of competition and its interaction with hydrodynamics is chosen deliberately to simulate a realistic mixing situation: in a perfectly mixed environment the dynamics of competition allow for the survival of the most fit species only, while in flows with non-chaotic advection, the coexistence of two species is possible but in spatially separated patches only, without real competition. It is thus the flow-induced imperfect mixing (Epstein, 1995) which can maintain coexistence in aquatic systems.

Because the reader of *Freshwater Biology* is unlikely to be an expert in hydrodynamics and chaos theory, in the following section, we present a qualitative description of the relevant physical process (details can be found in the references). Then we summarize previous results on chemical activity in chaotic advection. Based on these results, we propose a model for plankton coexistence. After that, the actual numerical algorithm is detailed. We then present the results obtained with the proposed model, and discuss why it leads to coexistence of competing species. Finally, the most important findings are summarized.

Passive advection in open flows

Chaotic advection in open hydrodynamical flows is a ubiquitous phenomenon. A flow is considered locally open if there is a net current flowing through the observation region (Lamb, 1932). It became clear in the last decade that passive advection, even in simple time-dependent flows, is typically chaotic (Péntek, Tél & Toroczkai, 1996; Károlyi & Tél, 1997). These flows, characterized by strong imperfect mixing, lead to the fractal spatial distribution of advected particles also observed in laboratory experiments by Sommerer, Ku & Gilreath (1996). For a review of the subject, see Péntek, Tél & Toroczkai (1996) and Károlyi & Tél (1997).

Let us now briefly summarize the most important characteristics of chaotic advection in open flows for the typical case of the flow around an obstacle. For medium inflow velocities, the flow in the wake is time-dependent but still spatially regular. These features are sufficient for the appearance of chaotic advection, and the presence of turbulence is not necessary.

Tracers advected past the obstacle are often temporarily trapped in its wake. This indicates the existence of tracer paths bounded to the wake. A detailed investigation shows that there is an infinity of periodic and non-periodic bounded paths in this regime. The set of all paths permanently trapped in the wake is called the chaotic set which forms, at any instant of time, a fractal cloud of points in the wake. Although the union of all these paths as a whole is an unstable object, there are exceptional initial tracer positions from where the flow advects the particles exactly onto this set. These positions form the stable manifold of the chaotic set, which extends into the far upstream region from the wake. Tracers being trapped around the chaotic set will eventually leave it along its unstable manifold, extending to infinity in the downstream region. This object can thus be considered as the avenue along which particles spending a long time in the wake are transported away. As a result of the fractality of the chaotic set, both types of manifolds are curves on which particles can move. This dynamical characteristic of the flow named as fractal foliation. Among these fractal objects the unstable manifold is the one directly observable by the naked eye and, therefore, is of primary importance: droplets of tracers injected into the flow upstream and being trapped in the wake for a while will trace out the unstable manifold for a long time (Sommerer *et al.*, 1996).

As a result of viscosity, there is a narrow boundary layer in the close vicinity of the obstacle's surface, within which the flow is laminar and slow. Of particular interest are the stagnation points on the obstacle's surface (cf. Fig. 1). The unstable manifold of some of the stagnation points is entangled in a very complicated manner with those of the chaotic set, which leads to an interesting and complex interplay between the effects of the boundary layer and that of the fractal manifolds in the wake.

Next, we illustrate the above observations in the simple case of a time-periodic flow around a cylinder. The flow is considered two-dimensional, i.e. the velocity field does not depend on the third coordinate, depth. Its incompressibility can always be assumed for velocities much below the speed of sound. A uniform inflow velocity can lead to a periodic detachment of vortices in the wake with a period T, which forms the so-called von Kármán vortex street (Shariff *et al.*, 1991; Jung & Ziemniak, 1992; Jung, Tél & Ziemniak, 1993; Ziemniak, Jung & Tél, 1994; Péntek *et al.*, 1995, 1996; Sommerer *et al.*, 1996; Toroczkai *et al.*, 1997). For numerical simplicity, we use an analytical model of this flow introduced by Jung *et al.* (1993).

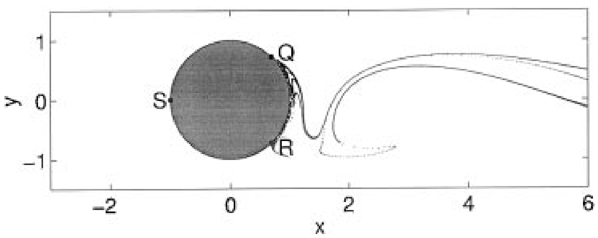

Fig. 1 Flow around a cylindrical obstacle. The fluid flows from left to right forming vortices (not shown) in the wake behind the cylinder. The advected tracers form the unstable manifold of the chaotic set in the wake of the cylinder, a snapshot is shown obtained at a given instant in a numerical simulation. Three basic stagnation points, Q, R and S are shown on the cylinder surface. The stable manifold of the whole chaotic set (not shown) foliates the inflow (or upstream region. Tracers close to the stable manifold get trapped in the wake for a long time, then leave it along the unstable manifold, leading them to the far downstream region. The smooth stable manifold of stagnation point S is also shown (dashed line).

Fig. 1 shows the unstable manifold in the wake at a given instant of time. Its complicated winding fractal structure is striking. Three stagnation points on the surface of the cylinder, denoted by Q, R and S, are also shown. The front stagnation point, S, acts as a saddle point separating the upper and lower part of the cylinder. It has its own stable manifold but this is a smooth curve lying close to the symmetry (x) axis. It leads tracers towards the cylinder's surface, thus they can penetrate into the boundary layer. This stable manifold is a kind of watershed between fluid particles moving around the disc of the cylinder along its upper or lower semicircle.

We emphasize that the qualitative features of the fractal patterns and of the boundary layer, which are essential for our study, are robust and can be found in any open, time-dependent flow. The shape of the obstacle, two-dimensionality, time periodicity and even incompressibility of the flow are considered only for convenience and ease of presentation.

Chemical activity in open flows

As a next step, we consider the advection of active particles in open flows. The particles are assumed to have no feedback on the flow, activity is assumed to be of chemical origin in the simplest possible form, when the reaction outcome is a kind of 'infection' (for chemical reactions in closed flows, see Metcalfe & Ottino, 1994; Neufeld, López & Haynes, 1999). This leads to a change of certain properties, e.g. colour, neighbouring particles. Particles with new properties are the products. As the effect of infection is most pronounced for particles staying for a long time around the chaotic set and for those leaving it around the unstable manifold, it is natural to expect that the products accumulate along the unstable manifold and trace out this fractal object.

It has been shown by Toroczkai et al. (1998) and Károlyi et al. (1999) that the unstable manifold of the chaotic set is the skeleton of the reaction. The newly born components cover the branches of the unstable manifold with a well defined average width. Thus, an effective fattening of the fractal takes place as a result of the activity of the tracers. This implies that, on linear scales smaller than this width, fractality is washed out, but a clear fractal scaling of the material (with the same dimension as that of the unstable manifold in the reaction free flow) can be found.

The permanent outflow of reagents is balanced by the chemical reactions and, most typically, a kind of steady state sets in after a sufficiently long time. In the case of time-periodic flows of period T, the asymptotic state is typically also periodic with T, i.e. the reaction becomes synchronized to the flow. Thus, a chaotic particle dynamics can be consistent with a non-chaotic reaction dynamics.

Interestingly, as a result of the small-scale inhomogeneities, the kinetic equations derived for the macroscopic distribution of the chemical components deviate strongly from those valid in well stirred containers. They reflect a strong enhancement of chemical activity catalysed by the spatial fractal structures.

A model of phytoplankton competition

We are interested in the dynamics of populations in relatively slow flows in the wake of rocks, islands or peninsulas. Depending on the size of the obstacle, for inflow velocities of about a few cm s^{-1}, the characteristic time T of the flow in the wake can be on the order of hours or days. The 'reproduction time' τ of the species investigated is on the order of T.

Our model of phytoplankton competition can be considered as an extension of the above mentioned model of chemical activity for active components competing for the same background material A. It is a simple kinetic model of reproduction and competition with point like particles (species) of type B and C. There is a constant inflow of material A into the system. Species B (C) catalysed by material A reproduce instantaneously at time intervals τ_B (τ_C), only if their centres come within a distance σ_B (σ_C) of particles of type A. The reproductive rates γ are proportional to σ/τ. As a result of the open character of the flow, the particles will drift downstream, therefore, leaving the mixing region of the wake. In addition, there is a spontaneous decay of individuals with mortality rates δ_B and δ_C. Two autocatalytic processes $A + B \xrightarrow{\gamma_B} 2B$, $B \xrightarrow[\delta_B]{} A$ and $A + C \xrightarrow{\gamma_C} 2C$, $C \xrightarrow[\delta_C]{} A$, thus describe the reproduction and competition process. It is well known that in well mixed homogeneous environments species with lower γ/δ ratio will be outcompeted (Gurney & Nisbet, 1998).

The above reproduction process is superimposed on our open flow around the cylinder. We emphasize that particles are again assumed to have no feedback on the flow. Therefore, in addition to the spontaneous decay (death) of the individuals, the number of microorganisms in a fixed region in the wake is also decreased by the advection dynamics. As the flow is open, individuals are transported away at a constant rate which is the same for all species in the wake.

The individuals are advected passively, and they interact with each other via competition for material A. Material A is the common limiting factor for both species B and C. It is worth mentioning that, in a purely chemical context, one is interested in the limit of a very small reaction lag, τ, corresponding to a time continuous reaction. In this work, however, we are interested in describing species whose reproduction time is comparable with that of the flow.

An important feature of the advection dynamics is their purely deterministic nature. This implies that we work at the limit of weak diffusion. We assume that the mutual molecular diffusion coefficient between any pair of the constituent particles is small. For the pair B–C, this is quite natural because both are planktonic. For pairs B–A and C–A, the limiting factor A could be the available habitat or some kind of chemical material as well. Therefore, even if no molecular diffusion is explicitly included in the model in the form of random forces, the reaction ranges σ_B and σ_C play the role of the inter-diffusion distance between B–A and C–A, respectively.

The numerical algorithm

For convenience, we carry out the simulations on a uniform rectangular grid of lattice size ε_0, covering both the incoming flow and the mixing region in the wake of the cylinder. This ε_0 also corresponds to the average distance between nearest-neighbour organisms. If there is an organism inside a grid-cell, it is always considered to be in its centre. The range of activity is bounded from below by the lattice size: $\varepsilon_0 \leq \sigma_B, \sigma_C$

The process starts with nearly all grid-cells containing A, the background material, for which the competition is going. Few grid-cells contain B or C at the beginning of the simulation. One iteration of the process consists of two steps. The first step models the advection of the replicators on the chosen grid, while the second step is the instantaneous active process (i.e., the 'replication') occurring on the same grid of cells. The advection phase also includes the random death of individuals, with a probability specific to its type, B or C. In fact, in any closed region considered, there is a loss of the individuals resulting from the advection and the finite life-time, but also a gain resulting from the reproductions.

If the different species (B and C) are advected into, or born in the same grid-cell, only one type of organism can survive in that grid-cell. In our simulations, a random process selects the survival at two stages. First, after the advection step, and later after the reproduction step, the coexistence of different kind of individuals in the same grid-cell is checked. If in a grid-cell both species are present, one of them is selected for survival with equal probability, the other dies out.

In fact, we checked our results with the most extreme selection rule also, when the organism with superior competition properties was always the winner in this conflict: the weaker organism was locally eliminated. Even this strong advantage was not enough in most cases fully to outcompete the inferior species.

Results

We turn now to the presentation of our numerical findings. Initially, we place two droplets of organisms from species B and C into the flow in front of the cylinder with $\sigma_B = 0.0067$, $\sigma_C = 0.0034$ and $\delta_B = 0.5$, and $\delta_C = 0.0001$. The radius R of the cylinder and the period T of the flow are taken as the length and time units. The fixed region of observation is a rectangle containing the cylinder and the wake. We monitor the number of organisms present in this region during the competition process. Fig. 2 displays the relative densities for both species, $N_B^{(n)}/N^{(n)}$ and $N_C^{(n)}/N^{(n)}$, vs. the number n of birth cycles (time). $N_{B(C)}^{(n)}$ denote the number of $B(C)$ particles, and we therefore have $N^{(n)} \equiv N_B^{(n)} + N_C^{(n)}$. After an initial rapid increase, the number of B and C cells becomes stationary in about 12 flow periods. A periodic time dependence sets in synchronized to the flow. This means that the number of individuals being born during a period is the same as the number of individuals disappearing as a result of the advection dynamics and of the mortality rate for both species. Similar steady states with non-zero numbers for both species has been found with several different parameters.

We emphasize that both species can coexist indefinitely in the wake of the cylinder in spite of their different γ/δ ratio. This property is a clear conse-

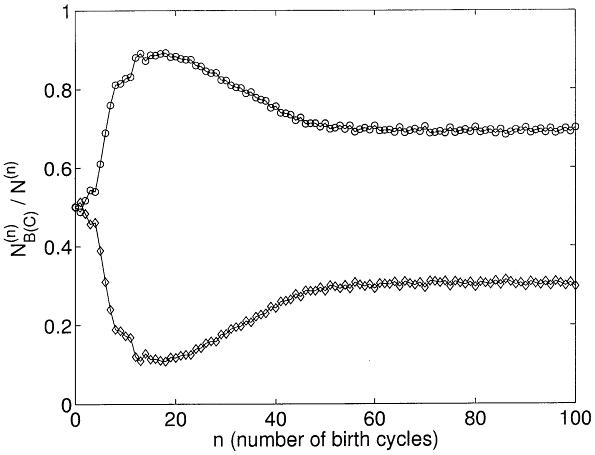

Fig. 2 The dependence of the number of B (circles) and C (diamonds) species present in the computational domain on time. Note the stationary time-periodic behaviour reached after about 12 birth cycles. The model parameters are $\sigma_B = 1/150$, $\sigma_C = 1/300$, $\delta_B = 0.5$, $\delta_C = 0.0001$ and $\tau = 1/5$, while the grid size is 1/300.

quence of the chaotic set, which traps the incoming particles for a long time in the wake. Both species *B* and *C* are pulled on the unstable manifold of the chaotic set, as their initial position overlaps with its stable manifold. Thus, both species *B* and *C* are trapped in the wake, and are accumulated along the filaments of the fractal unstable manifold. This leads to an enhancement of their activity, with both of them having increased access to the background *A* for which they compete. Along the fractal set, *B* and *C* can be separated quite efficiently by filaments of *A*. As a result of the imperfect mixing, the competition is reduced by spatial separation. This leads to the coexistence of the competing species for a wide range of parameter values.

Besides the number of individuals, it is instructive to see their spatial distribution as a function of time. Fig. 3 shows a series of snapshot of the organisms in the region of observation from zero up to time 20 periods of the flow. Note that in the asymptotic state species *B* covers the surface of the cylinder, while species *C* mainly occupies the wake.

A closer look reveals that, besides the chaotic set, the boundary layer also plays an important role in the coexistence of different species. The outcome of the dynamics strongly depends on the initial positions of droplets *B* and *C*. In general, the initial droplets of *B* or *C* might overlap with the stable manifold of the front stagnation point *S*. In our example, only the *B*

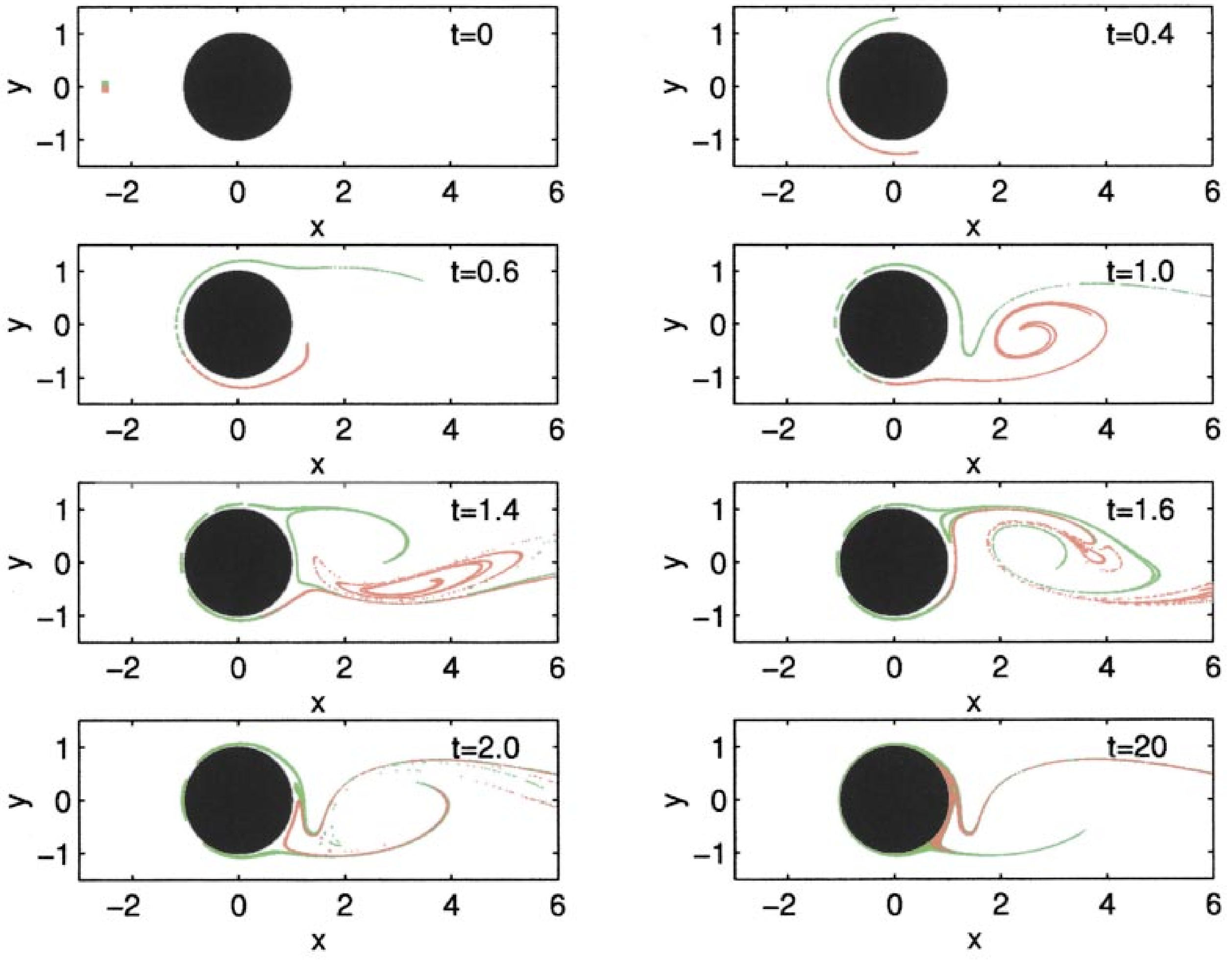

Fig. 3 The region of observation is shown at times $t = 0$, 0.4, 0.6, 1.0, 1.4, 1.6, 2.0 and 20 on the snapshots. Note the stretching and folding of the initially small droplets of species *B* (green) and *C* (red); they are eventually pulled along the unstable manifold. The stationary state is reached after a short time: the last two snapshots (taken at $t = 2$ and $t = 20$) are almost the same. Species *B* (green) occupies the boundary layer around the cylinder, while *C* (red) is trapped on the chaotic set in the wake. The model parameters are the same as in Fig. 2.

droplet overlaps with this line. B organisms, therefore, after reaching the front stagnation point, gradually spread along the surface of the cylinder and occupy the boundary layer. This results in a continuous supply of B to the wake from the boundary layer. The droplet of C was initially placed off the stable manifold of the stagnation point S, but overlapped with the stable manifold of the chaotic set. Individuals of C are thus outcompeted from the boundary layer, but trapped in the wake of the cylinder on the chaotic set. There is a strong competition here: B is supplied from the cylinder surface, and tries to outcompete C from the wake, while C tries to penetrate into the boundary layer from the chaotic set. These two effects balance each other in the steady state.

The species trapped around the front stagnation point has clear advantage, as it generates a kind of source for itself after occupying the boundary layer. The initial conditions can determine which organism can grow greater in number, but they do not effect the fact that both organisms can survive—provided that both organisms are initially overlapping with the stable manifold of the chaotic set, and thus, they have a chance to penetrate the wake. It can be seen in Fig. 2 that B, despite its inferior competitive properties ($\sigma_B/\delta_B < \sigma_C/\delta_C$), outnumbers C because of its better spatial position. This underlines the fact that, in the presence of imperfect mixing, the traditional picture is broken: the weaker organism can become dominant over the stronger one as a result of the advection dynamics. Besides the filamental structure, the boundary layer has an important role in maintaining species' coexistence. The speed of advection is very limited here and mixing is extremely slow. Individuals trapped in this area continuously transport new organisms for populations competing along the unstable manifold.

To illustrate the robustness of these effects, we carried out a series of further simulations. We now consider the case of equal 'reaction ranges' $\sigma_B = \sigma_C$, but different reproduction times, $\tau_B \neq \tau_C$. Here, τ_B and τ_C are to be understood as average reproduction times. While the dynamics of species B is the same as above, species C gives birth simultaneously with B, except that it may 'skip' every k-th replication when it does not reproduce itself. Thus, C is the weaker competitor, i.e. its average reproduction time τ_C is larger than that for B, $\tau_C > \tau_B$. In Fig. 4a, we show the same relative densities as in Fig. 2. Here, $\tau_C = 1.2\tau_B$. As one observes, the coexistence is present in this case as well, showing the robustness of the effect. The simulation corresponding to Fig. 4a was made with the full chaotic set, including the boundary layer. The next question one may ask is: could the long-term coexistence be caused solely by the boundary layer, where the flow is very slow, or is it generated by the fractal component of the wake? To answer this question, we made simulations where we 'eliminated' the boundary layer by cutting out a ring of width $\Delta r = 0.01$ from the dynamics around the cylinder (see Fig. 4b): if, during the advection, a particle approached the surface of the cylinder to a distance smaller than $\Delta r = 0.01$, it was completely discarded (it died out). The thicker (darker) line represents particle B, the other is C. We repeated the above simulations with various initial conditions and different reproduction times. We found the coexistence to be robust against all these variations over a finite range of the reproduction time deviation $\tau_B - \tau_C$, showing the enhancement of survival by the mixing dynamics working against the selection process, that otherwise would lead the weaker species to extinction in non-mixing (or equilibrium) environments.

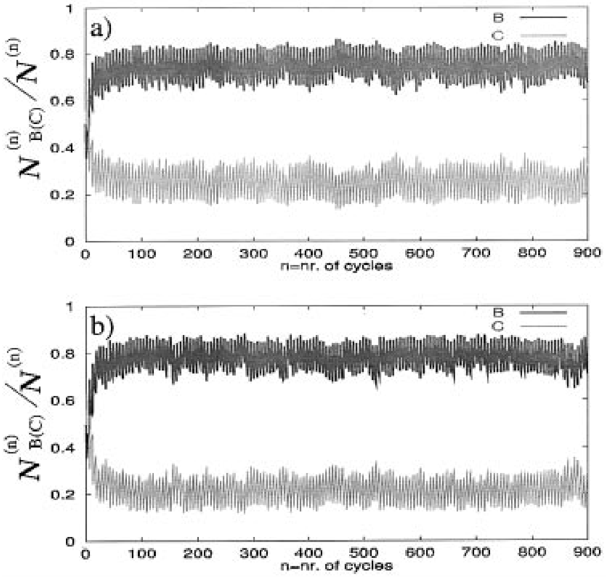

Fig. 4 The relative numerical density (a) with the full set, (b) with boundary layer excluded from the dynamics. In both cases, $\tau_B = 1$, $\tau_C = 1.2$ and $\sigma_B = \sigma_C = 0.005$. There is no spontaneous mortality in this simulation, i.e. $\delta_B = \delta_C = 0$.

Discussion

The above numerical simulations show that the coexistence of competing species is a generic feature and is expected to hold in a variety of open flows that exhibit chaotic advection.

The existence of a chaotic set is of primary importance. This set, and its fractal manifolds, ensures that all advected components, the species and the resource, evolve narrow filaments in the wake. These filaments of a given component intrude in originally wide filaments of some other component, thus splitting the latter into narrower filaments. This refining process goes on until a smallest filamental average width is reached, corresponding to a steady state. As a result of the permanent inflow, this property also holds for the resource. Thus, in the steady state, small regions of biologically relevant size can contain all components in considerable amount, which corresponds to a persistent coexistence of the species.

Besides the filamental structures, the boundary layer also has an important role in this coexistence. The speed of advection is very limited here, so mixing is extremely slow. Individuals, trapped in this area, continuously transport new organisms for populations competing along the unstable manifold. The biological importance of slow- and non-flowing areas of rivers is well known (cf. Young & Wallis, 1987; Reynolds, Carlin & Beven, 1991; Reynolds, Descy & Padisák, 1994). The biomass in these so-called 'dead zones' is much higher than in the main streams. Observations of Arístegui *et al.* (1997) support our view even more directly. They studied the chlorophyll distribution around the Canary Islands. According to remote sensing images, they concluded that chlorophyll content is high near and downstream of the islands. The fractality of chlorophyll distribution is obvious in the downstream region. We showed that our 'dead zone', the boundary layer around the cylinder, and the fractal filamental structure retains not only a higher concentration of individuals, but it enhances competitive coexistence.

Models assuming perfect mixing suggest that the result of population interactions can be forecasted merely from the population dynamical parameters. This view is criticized by terrestrial plant ecologists because the better competitor could be the species which arrives first or starts to grow earlier (Grime, 1979; Tilman, 1994). Similarly, the presence of algal species in the water are highly dependent on which phytoplankton 'seeds' are recruited from the sediment under a given environmental situation (Hansson, 1993). However, the spatial positions and timing of arrival of populations are the most basic factors that determine the relative density of competitors in our model system (cf. Fig. 2). The explanation is clear: to arrive at the unstable manifold and to get a good position in the boundary layer is crucial for the future success of the competitor.

It might seem to be contradictory that, while we studied open flows, oceans and lakes are closed systems, at least in a hydrodynamical sense. However, fluid parcels in oceans tend to return close to their inflow position only after years (after months in lakes). In contrast, our time scale on which physical conditions (the average temperature, nutrient supply, the light etc.) are approximately constant is, at most, some weeks. Consequently, advection can be considered open on our time scale.

It is worth noting again that, although our model flow is two-dimensional, this was just a technical assumption making the treatment easier. The basic ingredients leading to the conclusion of coexistence, however, do not rely either on this planar feature or on the model used here. In any three-dimensional flows producing chaotic advection, there are fractal filaments along which activity can be enhanced. On the other hand, filamental structures are present in two-dimensional turbulence (Babiano *et al.*, 1994). Therefore, we expect to see coexistence in similar competitive models of particles advected by either three-dimensional open chaotic flows or by two-dimensional turbulent flows. In fact, the chaos-induced imperfect mixing is the most essential property. Coexistence can also occur in closed chaotic flows (like those of lakes on long time scales), provided that the biological dynamics are sufficiently open (there is a continuous resource supply).

The keystone role of vertical transport in plankton ecology is well known (see e.g. Denman & Gargett, 1995). We would like to emphasize here that studying the small-scale physical characteristics of horizontal advection gives a new and more realistic insight into the population dynamics of aquatic systems.

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